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## General and Professional Biology



# GENERAL AND PROFESSIONAL BIOLOGY

*with Special Reference to Man*

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**SECOND EDITION**

**IN TWO VOLUMES**

**VOLUME II**

**INTRODUCTORY EMBRYOLOGY**

**(CHICK, FROG, and MAMMAL)**

**and**

**COMPARATIVE ANATOMY**

THE BRUCE PUBLISHING COMPANY  
MILWAUKEE, WISCONSIN

Second Edition

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Printed in the United States of America


21520



## PART I

# Introductory Embryology

(Chick, Frog, and Mammal)



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# CHAPTER I

## EMBRYOLOGY OF THE CHICK

### THE DEVELOPMENT OF THE EMBRYO BEFORE THE EGG IS LAID

**B**EFORE beginning the work in **Introductory Embryology** it is quite essential that the student turn back to earlier chapters and re-read what is said there on **mitosis**, **fertilization**, and the **histology** of the frog. Such a review will lay a foundation for the detailed study of the following pages.

When Comparative Anatomy is taken up in the next semester's work, it will be found that the Haeckelian law of biogenesis (also called the "recapitulation theory"), although untrue in its usual application, is a very convenient supposition in that it makes many points clear if we accept it as a working hypothesis. This so-called law is defined as follows: "All animals, during their embryonic period, pass through the same adult-stages that the various members of the race to which they belong, have passed." For practical purposes it is necessary to keep this theory in mind in the study of Embryology; for, it is the simplest way of bringing home to the student the fact, that in any biological study that is to be scientific, one must first study the more simple organisms and then compare such simple forms with those that are more complex—the so-called higher forms.

All living animals pass through a quite similar stage of development in their embryonic period, so that the next succeeding higher form practically possesses everything that the immediately next succeeding lower form possesses, **plus something additional**. And it is this "plus something" that we are trying to arrange in proper order when we study embryology.

The value of this is not always clear to the student. However, if he will remember that a human being and a chick pass through quite similar stages during their embryonic periods, the human being, however, developing further, he can understand how an obstruction may prevent any individual part of an organism from receiving the proper nourishment and environment, and thus cause such part to cease developing, and thereby to produce what is called a rudimentary structure. (Fig. 250.)

While all animals differ slightly from each other, there are certain **type-forms** in which the greatest differences can be clearly observed. Such type-forms, as commonly used in the laboratory, are the **dogfish**, as a representative of the cartilaginous fishes; the **frog**, as an example of amphibia; the **chick**, or **pigeon**, as an example of birds; the **turtle**,

as an example of reptilia; and the **cat**, **rabbit**, or **pig**, as an example of the mammals.

As we have been using the frog as a norm, or **standard type**, with which to compare the other forms studied, it would probably seem best



Fig. 250.

There is a membrane covering the pupil of the eye which, in man, normally disappears when the embryo is seven months old. In the case here shown portions of the membrane have persisted as an irregular network over the pupil. Such persistent structures are called rudimentary. (From a drawing lent by Dr. G. N. Brazeau.)

to begin Embryology with that animal. However, for the same reason that the frog was used as an introductory subject for study (because it can be procured easily and because it is a fairly complex form which possesses structures with which the student is already familiar), so, the hen's egg, which is much larger than that of the frog, can also be obtained easily and is already somewhat familiar to the student. In addition to this, the chick embryo develops upon the surface of the yolk, which makes the various germ layers very distinct, and serves much better than the frog as a beginning-type.)

The first and foremost point in the study of Embryology is **accuracy of observation**; the second is the obtaining of a clear **concept** of what has been observed; and the third is to show by **drawings** that the first and second points have been fully assimilated.

There is considerable need for legitimate imagination in embryological work, because the entire study of Embryology is for the purpose of giving the student a more or less comprehensive idea of the process through which, and by which, all the organ-systems in the body of living things **have come to be what they are**. The study of Embryology is, therefore, different from later work in pure anatomy, where each structure is definite, and where such structure is studied only after it is completely formed. In Embryology we see the beginnings and development of these later anatomical structures.

One should first take the **complete embryo**, and get a good grasp of the general structure. Then, **sections** must be cut at various intervals and studied microscopically. It must never be forgotten, however, that our imagination must constantly remind us that there are three dimensions to the living animal, and that what we are looking at in a section,

is but a series of **still pictures**, and that there is little value or meaning in such observation unless one can, with **imagination and logic**, plus **preceding biological knowledge**, build up a completed structure, so that the mind's eye can see the entire animal as it actually exists.

It must be remembered at this point that events which have taken place in the past, are the cause, or causes, of events that are now taking place, and that will take place later. This is as true in Embryology as it is in such a field as history, for example. This means that the various events of development are caused by preceding developmental events, and that these cause later steps in development in turn.

Another important point for the student to remember is that he must not only be able to recognize histologically the **type of cells** he may find in the section he is studying, but he must know the **definite location** in the complete embryo from which his section is cut.

The complete bird-like form of the chick can be clearly seen before the eighth day of incubation because all the principal changes have taken place by that time. It will, therefore, be understood that these changes are rather minute in their origins, for the eight-day embryo is only about seven millimeters in length. During, and after the eighth day, the changes which take place are primarily enlargements, or growth, of portions already present.

In the study of Embryology we are not only interested in the development of the chick from the egg, but we also wish to know how the egg came into existence.

The hen's egg is usually said to be a single cell. This is, however, only true if the egg is unfertilized.

As birds' eggs are laid with shells upon them, it is necessary that fertilization take place before the shell is formed. Fertilization in these cases is **internal**. It takes about 22 hours for the egg to have the layers of white laid down, and for the shell to surround it. (The layers of yolk are laid down before ovulation.) If the egg has been fertilized, the warmth of the mother's body has already caused development throughout these hours, so that by the time the egg is laid, the little chick is already approximately one, or one and a half, days old. There is a variation in the age because, if the hen's egg is ready for laying during the main part of the day, it is laid then, but if it is not ready for laying until, let us say, about four or five o'clock in the afternoon, it is retained within the mother's body until the following day, thus causing some embryos to be developed from ten to fifteen hours more than others.

The so-called spoiling of eggs is usually due to the fact that the embryo chick dies and then decays.

In birds, where the eggs leave the mother's body, the yolk must be quite large in order to furnish sufficient food for the embryo during the two or three weeks intervening between the time the egg leaves the mother's body and the time of hatching. In mammalian forms, the

egg remains extremely small because the nourishment of the embryo is derived directly from the mother.

During the very first day of incubation the outlines of the embryo are defined. During the second day a rather complicated series of folds appear, separating the embryo from the yolk. The embryo, however, remains in contact with the yolk-mass by a narrow stalk. The circulatory system now develops, through which nourishment is carried from the yolk-mass to the embryo. Embryonic membranes and appendages appear during the second and third days of incubation. These assist in respiration and also in forming a larger area from which the food supply may be brought from the yolk to the embryo.

Development usually begins at the head end and extends tailward, so that the brain and other head structures are often quite well developed when there is little semblance of any other well-defined structure toward the tail end. The chick usually makes a small opening in the egg shell on about the twentieth day of incubation, and from then on the lungs actually take in air and begin their regular external work, while on the twenty-first day the chick breaks entirely through the shell.

With this introductory general outline, we shall take up the study of the egg itself, working backward to its very simplest cell origin in the mother's ovary.

### THE EGG

The true ovum (Fig. 251A, v.), or egg-cell proper, is the large yolk or **vitellum**. This is surrounded by a tough **vitelline membrane**. The end of the ovum, where the embryo is to develop, is called the **animal pole**. It is nearly free from yolk, and appears at the time of laying as a circular whitish area, known as the **blastoderm** (Fig. 251, b), and measures from three to four millimeters in diameter. As the animal pole is not so dense as the surrounding material, it is always found on top of the yolk, no matter which way the entire egg is turned, provided, of course, that the yolk is free to rotate.

The more central portion of the animal pole is rather translucent, or **pellucid**, and, therefore, is called the **area pellucida** (Fig. 251A, c). This central portion is surrounded by a whitish, or **opaque**, region called the **area opaca**. The yolk itself is called **deutoplasm**, and is divided into two types of material, **white and yellow yolk**. The white yolk is thickest in the region just below the blastoderm, where it is shaped like a flask, as shown in the figure. It extends to the center of the yolk. It will be noticed that the yolk is thus arranged in various **concentric layers**. A layer of thick yellow yolk alternates with a thinner stratum of white yolk. The two types of yolk differ in physical characteristics and in chemical composition.

The vitellus, or true egg-cell, alone is formed in the ovary. Such structures as develop within the ovary proper are called **primary**. Structures, such as **chorionic membranes** (found in most of the higher

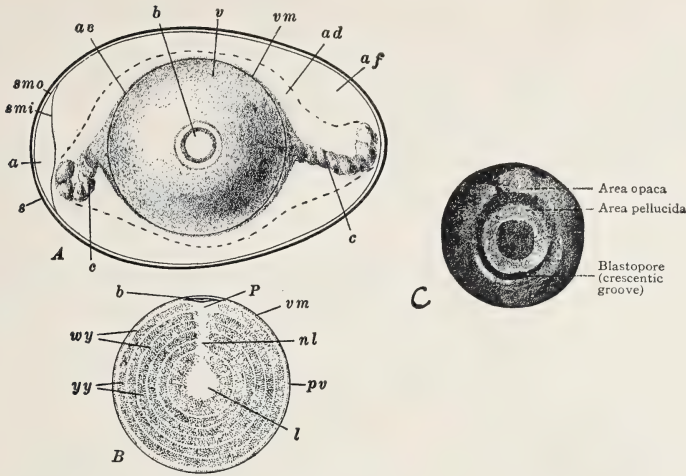


Fig. 251.

Semidiagrammatic illustration of the hen's egg at the time of laying. *A*. Entire "egg." *B*. Diagram of a vertical section through the vitellus or ovum proper, showing the concentric layers of white and yellow yolk. *a*, Air chamber; *ac*, chalaziferous layer of albumen; *ad*, dense layer of albumen; *af*, fluid layer of albumen; *b*, blastoderm; *c*, chalazae; *l*, latebra; *nl*, neck of latebra; *p*, nucleus of Pander; *pv*, perivitelline space; *smi*, inner layer of shell membrane; *smo*, outer layer of shell membrane; *v*, vitellus or "yolk"; *vm*, vitelline membrane; *wy*, layers of white yolk; *yy*, layers of yellow yolk. *C*. Surface view of Blastoderm of unincubated hen's egg. (*A* and *B*, after Marshall; *C*, after Hertwig.)

forms), are known as **secondary** structures, while those particular regions which are formed by **accessory reproductive organs**, such as the white of the egg and the shell, are said to be **tertiary structures**. The white of the egg is composed of albuminous matter which is chemically quite complex. It will be remembered that the protoplasm in all living cells is largely albuminous.

Toward each end of the newly-laid egg, one finds a dense, opaque twisted cord, extending through the white of the egg from opposite sides of the yolk toward the apices of the shell. These twisted cords are called **chalazae** (Fig. 251A, c). They are continuous with a very thin, dense layer of albumen surrounding the yolk. This thin layer is called the **chalaziferous layer**. It is generally assumed that the chalazae assist in holding the yolk in position, though this has been disputed by several biologists, primarily because the ends nearest the shell are not attached. Immediately outside the chalaziferous layer there is another thick, dense layer of albumen, and superficial to this is a still thicker layer of a more fluid albumen. The hard-boiled egg in which the albumen has coagulated lends itself well for the observation of these various layers. Usually, in observing such hard-boiled eggs the albumen is seen to be arranged in **spiral sheets**.

The ovoid shell which surrounds the entire egg is quite resistant to gradually applied pressure, but easily broken if the blow be sharp. The shell in turn is covered superficially by a thin cuticle perforated by many pores. The main substance of the shell is made up of loosely arranged

particles of carbonates and phosphates of calcium and magnesium. The inner surface of the shell is composed of a thin but dense layer of inorganic salts. After the shell has dried, it is quite porous, thus making the passing of gases and water-vapor quite easy.

There is a tough **shell membrane** lining the inner portion of the shell. It is composed of a double sheet of fibrous connective tissue which separates at the blunt end of the egg into an air space, becoming larger as time goes by.

## THE REPRODUCTIVE ORGANS OF THE FOWL

One obtains a more thorough understanding of the development of the egg in the ovary if a review of the entire reproductive organs is

undertaken. The reproductive organs of the fowl do not develop equally on each side, though they begin developing symmetrically. The right ovary ultimately degenerates, and so far as we know does not function. The **left ovary** (Fig. 252) and **oviduct** alone carry on the work of the organs. The left organs, therefore, become quite large.

A microscopical section of the ovary shows this organ to be composed of a great quantity of **ova**, each ovum being contained in a **Graafian follicle** (Fig. 253). The ovary itself is suspended from the dorsal abdominal wall by a double fold of the peritoneum called a **mesovarium**.

In the hen, the ova vary in size from a very small cell up to the full sized yolk. The **oviduct** is large, thick-walled, and muscular, being convoluted, and having a different structural form in the different parts. The oviduct carries eggs from the ovary to the **uterus**. The abdominal opening of the oviduct is rather wide, flaring, and funnel-shaped, and comes in close contact with the ovary. This opening is called the **ostium** or **infundibulum**, or the **fimbriated opening**. This last name is due to its fringe-like mar-

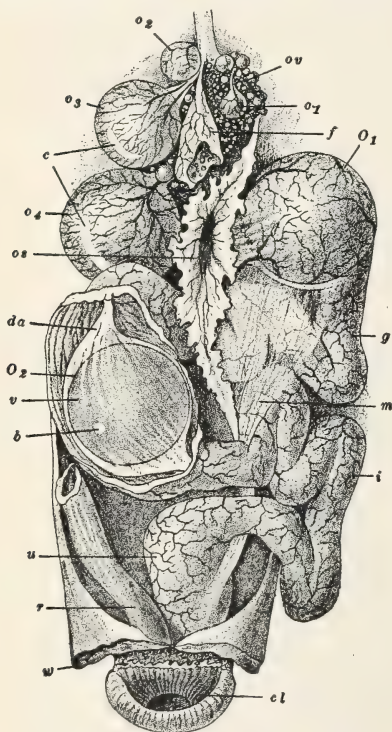


Fig. 252.

The reproductive system of the fowl. The figure shows two eggs in the oviduct, whereas normally only one egg is in the oviduct at a time. *b*, Blastoderm; *c*, cicatrix; *cl*, cloaca; *da*, dense layer of albumen; *f*, empty egg follicle from which the ovum has escaped; *g*, glandular portion of oviduct; *i*, isthmus; *m*, mesovarium; *o<sub>1</sub>-o<sub>4</sub>*, ovarian ova in various stages of growth; *O<sub>1</sub>*, ovum in upper end of oviduct; *O<sub>2</sub>*, ovum in middle portion of oviduct (the oviduct has been cut open to show the structure of this ovum); *os*, ostium or infundibulum; *ov*, ovary containing ova in various stages of growth; *r*, rectum; *u*, uterus; *v*, vitellus; *w*, ventral body wall, opened and reflected. (From Duval.)

gin. This region of the oviduct is thin and muscular and lined with cilia. The oviduct proper, into which the ostium leads, is known as the **convoluted glandular portion**, which is followed by a short, third portion called the **isthmus**. It is after passing through the isthmus that the egg enters the so-called **uterus**, which is merely a dilated portion of the glandular tube. The uterus in turn opens into a short **terminal region**, a rather thin-walled **vagina**, and this again opens into the **cloaca**, just dorsal to the opening of the rectum.

It is easier for the student to understand a developmental history of the egg if it be thought of as passing through three periods. First, from the beginning of the development of the ovum to the time of **ovulation**. Second, from the time of ovulation through the period of **fertilization**, and third, from the beginning of **cleavage** to the time the egg is laid.

**First Period.** (From the beginning of the development of the egg to the time of ovulation.) Most animals produce a large number of eggs within a very brief period, while in the hen there is a long period of egg formation and laying, which extends over several months, after which there is a period of almost complete cessation. Undoubtedly the reason for this is that, when an egg becomes so large as that of the hen, which

requires so much food in its making, it is a considerable drain upon the animal, and secondarily, there isn't room enough in the body of an animal no larger than a hen for many eggs of such size. However, the fact that the hen's ova develop in the way they do, makes it possible for us to observe almost a complete succession of developmental changes from the minute forms up to the fully developed egg.

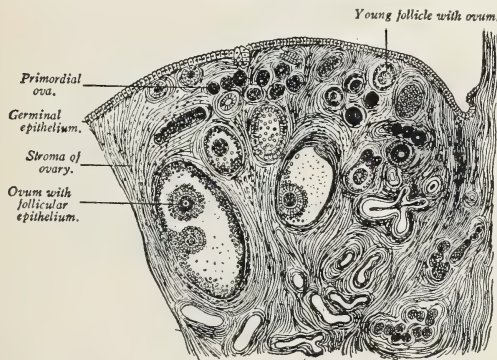


Fig. 253.

Section from ovary of adult dog. The more or less star-shaped figure on the right is a collapsed follicle with its contents. Below and at the right are seen the tubules of the Parovarium. (After Waldeyer.)

Biology, we learned that very early in an organism, especially in triploblastic forms, the germplasm and somatoplasm differentiate. A few cells are set aside in the innermost portion of the body of the growing embryo for reproductive purposes. The development of the germplasm in the growing embryo is called **oögenesis** in the female and **spermatogenesis** in the male.

## OÖGENESIS

The process by which the eggs, already present in the ovary of the new-born chick, originally came to be what they are, is known as

**oögenesis.** The first event in oögenesis is known as the **multiplication of the oögonia**. This occurs during the embryonic period of the animal. There are two types of cells which develop from the original primary cells set aside for reproductive purposes. How and why these differentiate in the way they do, we do not know, but we do know that there is a differentiation.

As soon as these original cells begin to divide, some of them develop into centrally located eggs or ova (Fig. 254), while others, known as **germinal epithelium**, surround the more centrally located ova and form a sort of case, or capsule, around them. The primitive egg surrounded by this epithelial case is known as an **oögonium**. Some of the primitive eggs leave the epithelium and pass into the stroma of the ovary. There they degenerate. Those remaining, however, begin enlarging even while they are dividing and multiplying. The epithelial cells also divide very rapidly, forming long strands or cords which in turn extend into the stroma. There comes a time when these primitive ova, or oögonia, stop multiplying; they are then called **primary oöcytes**. At this time the strands, or cords, of germinal epithelium break up into little groups, sometimes called **nests**. Each nest consists of a single primary oöcyte (Fig. 255) surrounded by a number of the original epithelial cells. These latter cells form a definite case surrounding the oöcyte. The case thus formed is called the **primitive egg follicle**. This final arrangement takes place within a few days after hatching. It will thus be seen that all the eggs which enlarge, ripen, and pass out of the ovary are merely enlarged and developed primary oöcytes.

Both the nucleus and the cytoplasm of the egg cell now begin to enlarge, and yolk granules are laid down all about the centrally located nucleus as well as throughout the cytoplasm, **except in the peripheral region**. This region remains comparatively free from yolk. At the point where the ovum, or follicle, is attached (Fig. 256), there is a thicker

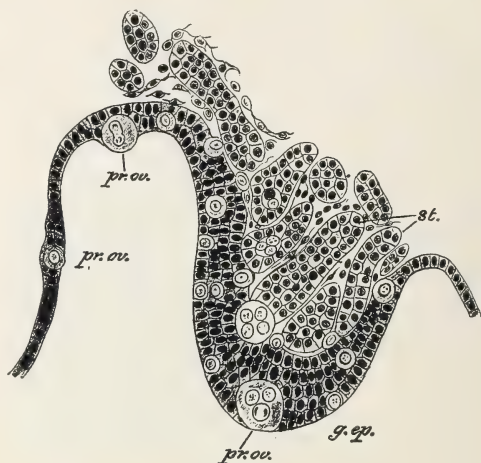


Fig. 254.

Section of the Germinal Epithelium and Adjacent Stroma in a Chick-Embryo.

*g.ep.*, germinal epithelium forming a thickened ridge-like projection; *pr.ov.*, primitive ova of various sizes, some in the germinal epithelium and others somewhat beyond the limit of this epithelium; *st.*, strands of cells which have grown from the germinal epithelium, and one of which appears connected with an enlarged primitive ovum. (From Semon.)

portion in the periphery known as the **germinal disc or spot**. As soon as the ovum reaches a diameter of about five-tenths of a millimeter, the nucleus migrates into the germinal disc, where it remains as long as the egg continues in the ovary. An important point to remember is that the animal pole of the ovum is toward the attached surface, that is, at the point where the nucleus is located.

From this time onward, the yolk accumulates very rapidly. The surface of the ovum is in the form of a **zona radiata** (Fig. 256, B), in which there are many pores through which nutritive substances may easily diffuse from the follicle cells. These follicle cells may, therefore, be called **nurse cells**.

When the follicle has completed its growth, it becomes somewhat membranous. Directly opposite its point of attachment there are very

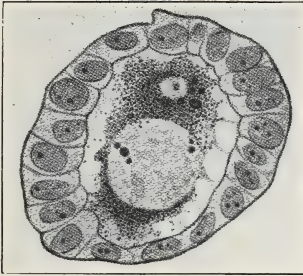


Fig. 255.

Young Mammalian Oocyte surrounded by a single layer of Follicular Cells. (Van der Stricht.)

Showing attraction-sphere, centrosome, and mitochondria.

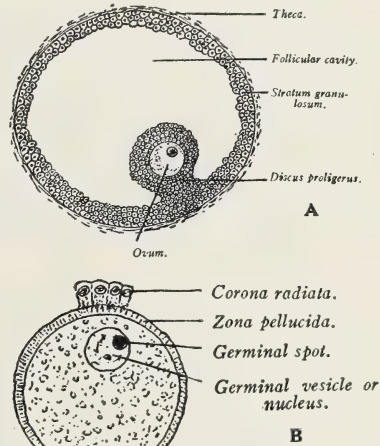


Fig. 256.

A, ripe Mammalian Graafian follicle. B, ovum.

few blood vessels, and it is at this point that a modification takes place in the appearance of a band, known as the **cicatrix**. It is at the cicatrix that the follicle ruptures to permit the escape of the egg into the oviduct.

The nucleus lies flat against the vitelline membrane, and becomes very large just before the egg leaves the ovary. It is then called a **germinal vesicle**, because the chromatin condenses, which leaves the nucleus appearing as a large clear hollow spot. The nuclear wall now breaks down and forms the first **polar spindle**. This rotates into position and the primary oöcyte is ready for its first maturation division, and later, for ovulation.

**Second Period.** (Ovulation, maturation, and fertilization.)

The coördination of different functions in the body is well shown by the fact that at about the time a completed egg is ready to pass into the oviduct, the region of the ostium of the oviduct becomes very active and actually seems to grasp the ovarian follicle which contains the primary oöcyte. This may be due to muscular, or ciliary, action or it may be a combination of both. The follicle then ruptures, permitting the egg to be thrown out. It seems that the pressure exerted by the contraction of the fringed end of the ostium may have something to do with such rupture. The throwing out of the eggs from the follicle is called **ovulation**. The oöcyte always enters the infundibulum of the oviduct with its chief axis transverse to the long axis of the oviduct, and throughout its entire passage down the tube, this relation is retained.

After the sperm have been injected into the female, they make their way up the oviduct toward the ovary, seeming to gather at its end. They may remain alive and function for at least two weeks, sometimes even longer. It will thus be noted that as soon as the egg has been discharged from the follicle and has been taken into the oviduct, there are millions of sperm floating about in the fluid surrounding it. A single egg of the hen, unlike that in most animals, has from five to twenty-four spermatozoa enter it. Such a process is known as **polyspermy**. Polyspermy is abnormal in most animals, but it is the normal condition in the hen. The egg is now **fertilized**. The sperm apparently affords the stimulus which causes the egg to begin dividing and to form an embryo.

The egg, after the entrance of the various spermatozoa, is not yet completely mature. A process of **maturation** now takes place.\* This means that the egg divides into a larger and a smaller portion, both of which portions may again divide into two parts. All of the smaller portions degenerate, one large portion alone developing into a complete, fertilized, hen's egg. The purpose of the small **polar bodies** (as the degenerating portions are called) is to throw off one-half of the chromatin in order that the new-born young may be a normal individual like its parent, as explained in our studies of mitosis, maturation, and genetics.

After the **second maturation division**, the remaining nucleus unites with a single sperm nucleus to form the **first cleavage spindle**, and the egg is now ready to begin dividing and form a true embryo.

**Third Period.** (From the beginning of cleavage to the time the egg is laid.)

It must be remembered here that the fertilized egg, which is to become the embryo, is present in the hen's body quite a number of hours before the egg is laid; in fact, from one to one and a half days before the various layers of white and shell have encircled it. The heat from the

\*In many animal-forms maturation takes place before ovulation; in some it begins before ovulation but is not completed until some time after.

mother's body has caused the embryo to begin to form, so that by the time the egg is laid, the embryo is already many hours old. It is, therefore, essential that the student understands in detail, exactly what has already happened in the mother's body before the egg passes to the outer world.

The **first cleavage furrow** can be seen about three hours after the ovum has been discharged from the follicle. During this period the egg has passed along the entire glandular portion of the oviduct. The glands themselves have secreted the most dense portions of albumen and also the chalazae. The yolk was already laid down **before ovulation**. The egg is carried along principally by **peristaltic action** of the walls of the oviduct. Then, as the egg itself rotates, the germ disc comes to describe a spiral path, which explains the spiral arrangement of the albumen around the yolk. The egg then traverses the isthmus for approximately an hour, where the shell membrane is secreted over the dense albumen. The fluid layer of albumen is secreted both in the isthmus and the upper part of the uterus. The fluid layer of the albumen passes through the shell membrane which has already been laid down, and it takes from five to seven hours after the egg enters the uterus before this is completed. But, before this takes place, the shell substance itself has already begun to be laid down on the shell membrane. Usually twelve to sixteen hours are necessary to complete the passage through the uterus and vagina. At the end of this time **twenty-one to twenty-seven hours have already elapsed since ovulation took place**. Gastrulation has begun, and the egg is laid.

We have already mentioned that, if the egg reaches the vagina, ready to be laid, during the main portion of the day, it will be laid on that day. If, however, it should be ready for laying after four or five o'clock in the afternoon, it will be retained in the vagina until the following day, thus causing some embryos in freshly-laid eggs to be approximately twelve hours older than others. It is for this reason that there is always considerable variation, even when eggs have been incubated for the same number of days.

**TABLE (After Kellicott) SHOWING THE CHIEF EVENTS IN THE EARLY HISTORY OF THE HEN'S EGG**

Hours after Ovulation	Location in Oviduct	Action of Oviduct	Action of Germ Disc
0	Infundibulum	Reception of Ovum	Maturation and Fer- tilization.
0 to 3	Glandular Portion	Secretion of chala- zae, chalaziferous and dense albumen layers.	First cleavage fur- row.

3 to 4	Isthmus	Secretion of shell membrane and fluid albumen.	Formation of eight cells.
4 to 21 (27)	Uterus and Vagina	Secretion of shell and fluid albumen. Retention prior to laying.	Gastrulation begun, or completed if egg is long retained.

With what has just been said in mind, the developmental processes of an embryo become more understandable. The unicellular germ disc is composed of a very definite area at the animal pole. The disc itself is about three millimeters in diameter, and less than five-tenths millimeters in thickness. Directly beneath this disc, there is a merging of the protoplasm with the white yolk. This well-marked region is called the **nucleus of Pander** (Fig. 251, P), and this connects the central white yolk by a narrow stalk called the **latebra**. It is necessary to study all the figures carefully to understand these and successive terms, and to grasp the relationship of each to the other.

There are two regions in the disc itself: the larger central portion

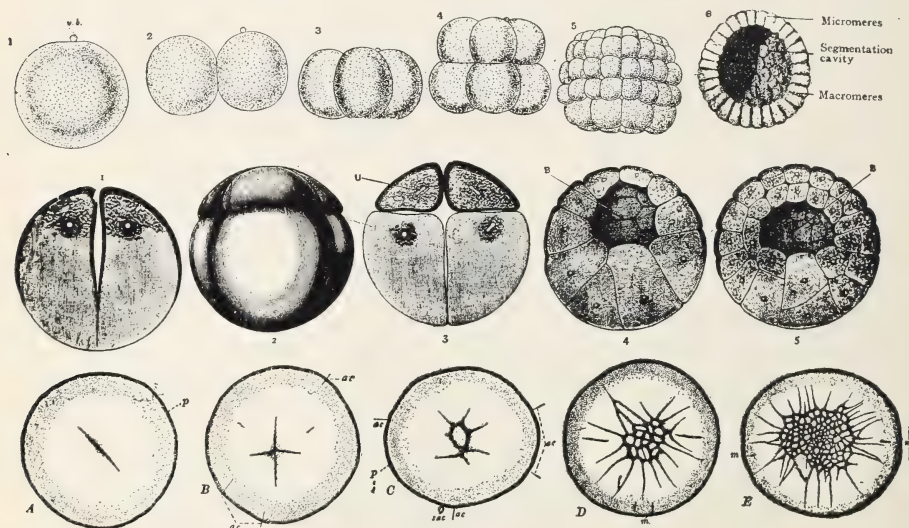


Fig. 257.

Cleavage. Upper Row, *Amphioxus*. (After Hatschek.) 1, Unfertilized egg; 2, stage of two blastomeres; 3, stage of four blastomeres; 4, stage of eight blastomeres; 5, stage of seventy-two blastomeres; 6, section of blastula; *p.b.*, polar body. Middle Row, Frog. *B*, segmentation cavity. *v*, nucleus. Lower Row, Hen's egg. (After Patterson.) Surface views of the blastoderm and the inner part of the marginal periblast only. The anterior margin of the blastodisc is toward the top of the page. *A*. Two-cell stage. About three hours after fertilization. *B*. Four cells. About three and one-fourth hours after fertilization. *C*. Eight cells. About four hours after fertilization. *D*. Thirty-four cells. About four and three-fourths hours after fertilization. *E*. One hundred and fifty-four cells upon the surface; the blastoderm averages about three cells in thickness at this stage. About seven hours after fertilization. *ac*, Accessory cleavage furrows; *m*, radial furrow; *p*, inner part of marginal periblast; *sac*, small cell formed by the accessory cleavage furrows.

which is to form the **blastoderm** proper, and the narrow denser area known as the **periblast**, which forms the outer margin. The periblast is continuous with the membrane covering the yolk, peripherally.

In the center of the germ disc, the first cleavage furrow appears. (Fig. 257.) It is short and shallow, running about one-half the diameter of the disc. We do not know whether the first cleavage extends directly through the central portion of the embryo. The main embryonic axis lies almost at right angles to the long axis of the whole egg, the head end of the embryo being directed toward the left when the sharp end of the egg is held pointing away from the observer. The first cleavage plane does not seem to have any definite relation to either of these axes.

The second cleavage is also vertical and almost at right angles to the first, so that we have four adequal cells, all, however, incomplete. The third cleavage appears about an hour after the first. This is usually parallel with the first. It divides the disc into two rows of four cells each. This cleavage may be quite irregular in form, and from now on it is impossible to tell exactly how and when, in relation to time especially, these egg cells divide. Consequently, after they have divided and formed sixteen cells, all of these cells are very irregular, and there is a tendency in the fourth cleavage plane to separate the eight cells into a **central** and a **marginal** group.

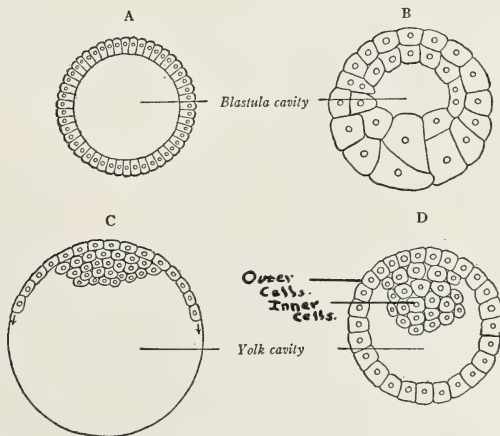


Fig. 258.

Diagrams showing the blastulae: A, of *Amphioxus*; B of frog, and C, of chick; D, blastodermic vesicle of mammal. (After Semon.)

The group of **central cells** becomes circumscribed and must not be confused with the **marginal cells** which remain incomplete both below and distally, retaining their connection with the periblast. These central cells have been separated by a horizontal cleavage plane, and this cleavage plane separates the more superficial cellular elements from

the underlying undivided substances, leaving a little space, which is the beginning of the **segmentation cavity** or **blastocoele** (Figs. 257, II B, and 258). The undivided substance beneath is called the **central periblast**, the original periblastic region being now known as the **marginal periblast**. Both of the periblastic regions retain their connection with each other peripherally in the deeper regions of the marginal cells.

The question that may arise here is, "What has become of the accessory or supernumerary spermatozoa?" Between the time of fertilization and the first cleavage, these have formed nuclei which migrated to the outlying portion of the blastodisc. There they probably divided once or twice to form small groups of daughter nuclei. There even seems to be an attempt of the cytoplasm to divide, and sometimes short superficial growths are actually formed. These are called **accessory cleavages**. They can be seen during the four and eight cell stage, usually radial in direction, lying just across, or outside, the margin of the blastodisc. No true cells, however, are formed by such cleavages. The accessory sperm nuclei all degenerate rather rapidly, the accessory cleavages fading away, so that by the time the embryo has reached the thirty-two cell stage, no traces of these accessory structures can be found at all.

As cleavage continues, the number of central cells increases very rapidly by the marginal cells, dividing and being added to the central cells, although the central cells divide likewise. This latter multiplication is very rapid, the cells diminishing in size. For example, cleavages appear in the central cells, causing the roof of the blastocoele to become several cells in thickness. No cells are added to the germ disc from the floor of the segmentation cavity. The continual cutting off of central cells from the marginal cells causes these latter to be considerably shortened, until finally they are limited to the extreme margin of the blastodisc only.

After division has taken place so that two or three hundred cells have been formed, there are intercellular furrows extending out into the marginal periblast. Up to this time, there have been no nuclei whatever in either central or marginal periblast, but two areas, which are continuous, now become converted into a nucleated syncytium. Our knowledge of this developing process comes from the study of the pigeon. It has not been worked out in the chick. The process is somewhat like this: The marginal cells have become spherical in form, by having the central cells cut off from them. Their nuclei now divide, although the cytoplasmic divisions are either completely lacking or do not completely divide. The free nuclei, therefore, become quite extensive in the margin of the blastodisc, and as these nuclei continue multiplying, they wander off into the marginal periblast so that nuclei are scattered about quite thickly, though the structure itself is non-cellular. Some of the nuclei also migrate inward below the blastodisc, so that the central periblast is likewise converted into a nucleated structure

with the exception of the middle area above the nucleus of Pander. This area continues to remain free from nuclei; in fact, what is later to be known as the **germ wall**, is partly composed of the nucleated rim of the periblast.

The blastoderm, which is rather circular, extends radially, both on account of the growth of its own cells, and by the addition of cells from the marginal periblast. The original region of the blastodisc becomes thinner and transparent. It is then called the **area pellucida**. The circular margin, which is derived from the periblast, is called the **area opaca**. The ring-like periblast keeps on growing, while additional nuclei are formed peripherally. At the same time, the periblast is contributing cells to the blastoderm also, so that the blastoderm steadily increases in diameter. The inner nucleated margin of the periblast, which later becomes cellular, contributes to the later extra-embryonic tissues and is called the **germ wall**. The cells of the blastoderm later extend peripherally so that they overlap the inner margin of the germ wall, to form a narrow region, transitional between pellucid and opaque areas.

It should be noted here that the lower surface of the periblast is directly continuous with the yolk mass, and peripherally it is continuous with a very thin superficial tissue of protoplasm. This latter is also often referred to as a part of the germ wall.

As soon as the blastoderm has become thinned out as mentioned above, the **blastula stage** is completed.

It is well at this point partially to summarize the development through the morula and blastula stage before taking up gastrulation.

### THE MORULA STAGE

While text-books usually speak of an "end" to the segmentation process, it must not be supposed that the cells of the embryo stop dividing. The whole process is continuous, and the word "end" here means only that the general process of cell-division is now "general" no longer, but that **differentiation** begins. The ending of the segmentation stage means only that one can from this period on, find a grouping or aggregation of cells which are not all alike.

In eggs in which there is but little yolk (therefore not in birds' eggs), the segmentation results in a rounded, closely packed mass of embryonic cells (**blastomeres**), called a **morula**. This name has been given such a cell mass because it resembles a mulberry. This morula stage, in eggs with little yolk, corresponds to the stage at the "end" of segmentation in the chick embryo. At this time the embryo is a simple disc-shaped mass of cells, several layers in thickness. This whole mass is the **blastoderm**. It lies closely applied to the yolk.

The cells in the center of the blastoderm are smaller and quite clearly defined, while the surrounding or peripheral cells are flattened, larger, and in more intimate contact with the yolk beneath.

## BLASTULATION

The chick embryo remains in the morula stage for a very short period, then there is a rearrangement of cells preliminary to the blastula formation. First, a cavity forms beneath the blastoderm due to the smaller central cells separating from the underlying yolk. The outlying cells remain attached. This space is called the **segmentation cavity**, or **blastocoel**, while the marginal area of the blastoderm, which remains attached to the yolk, is called the **zone of junction**. As soon as the segmentation cavity is thus formed, the embryo is said to be in the blastula stage.

From Figure 259, which shows only the blastoderm and a portion of the yolk (the yolk being about three feet in diameter at this magnification), a good understanding may be had of the difference which a larger amount of yolk makes in the blastula-formation.

In eggs with little yolk, a definite morula or solid sphere of cells can easily form, which may then develop into a hollow sphere or **blastula**. But in eggs with a large quantity of yolk, as in the pigeon and the chick (Fig. 258), the blastomeres are forced to grow on the surface of the

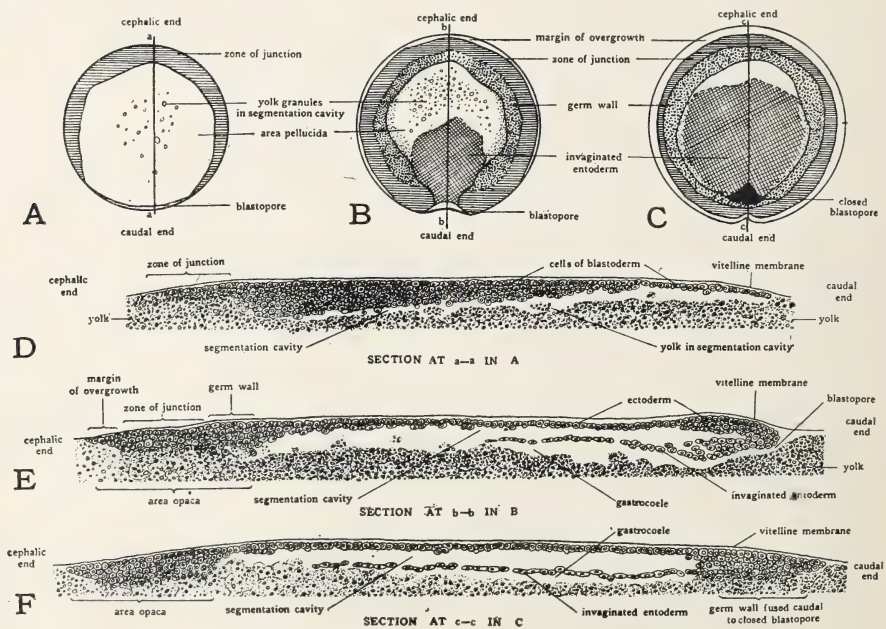


Fig. 259.

Diagrams to show various stages in the gastrulation of a bird embryo. In the surface-view plans, the blastoderm is supposed to be transparent so the underlying structures may be located. *A*, surface view of blastoderm, just before invagination; *B*, surface view of blastoderm, invagination well advanced; *C*, surface view of blastoderm at end of gastrulation; *D*, vertical section through blastoderm of stage represented in *A*; The plane of section is indicated by the line *a-a* in *A*. *E*, vertical section through blastoderm of stage represented in *B*. The plane of the section is indicated by the line *b-b* in *B*. *F*, vertical section through blastoderm of stage represented in *C*. The plane of the section is indicated by the lines *c-c* in *C*. (From Patten, after Patterson's figures for the pigeon.)

yolk, which is the mechanical reason for the disc-shaped blastoderm being where it is and what it is in the bird's egg. That is, if the large yolk of a bird's egg were removed and the blastoderm were allowed to assume the spherical shape which it would naturally take due to surface tension, there would be a decided similarity between the disc-shaped blastoderm and the ordinary morula stage of eggs with little yolk, such as in *Amphioxus* and in man.

Not only does the great quantity of yolk make this change in the morula stage, but it is evident that a large amount of yolk does not permit a simple hollow sphere formation by any method of cell arrangement. Nevertheless, the central cells do separate somewhat from the yolk and form the slight segmentation cavity mentioned above.

Imagining, now, that the yolk could be removed and the ends of the blastoderm drawn together, we should have a true blastula form of the simpler type.

### GASTRULATION

It is essential that one remember that a large quantity of yolk will make a considerable change in the process of gastrulation. The simpler

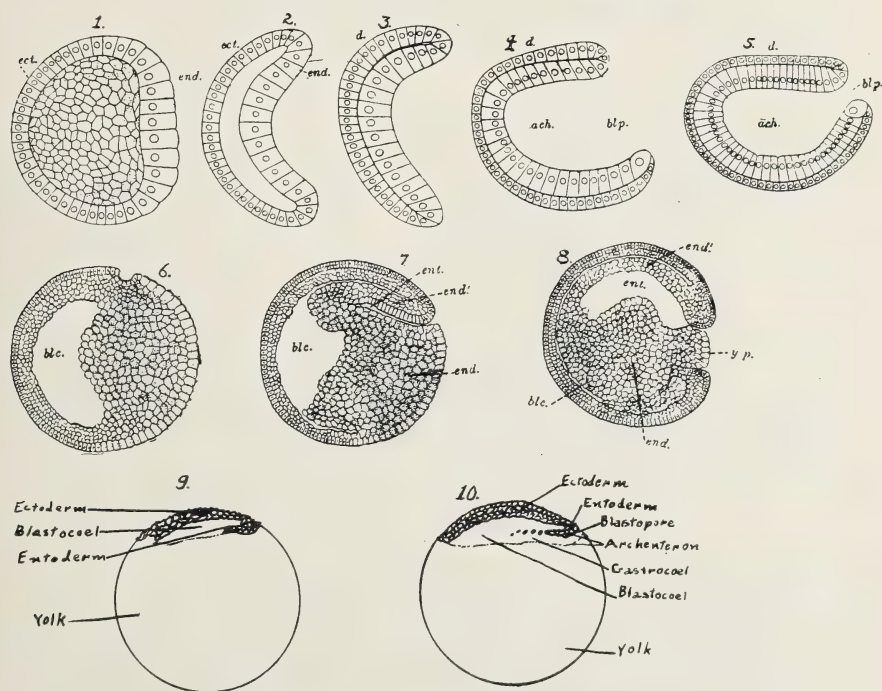


Fig. 260.

Gastrulation in egg with different quantities of yolk. 1-5, *Amphioxus* (little yolk); 6-8 Amphibian (moderate amount of yolk); 9-10, Birds (large amount of yolk); blc., blastocoel; d., future dorsal side; ect., ectoderm; end., entoderm; ach., archenteron; blp., blastopore; y.p., yolk plug. (After various authors.)

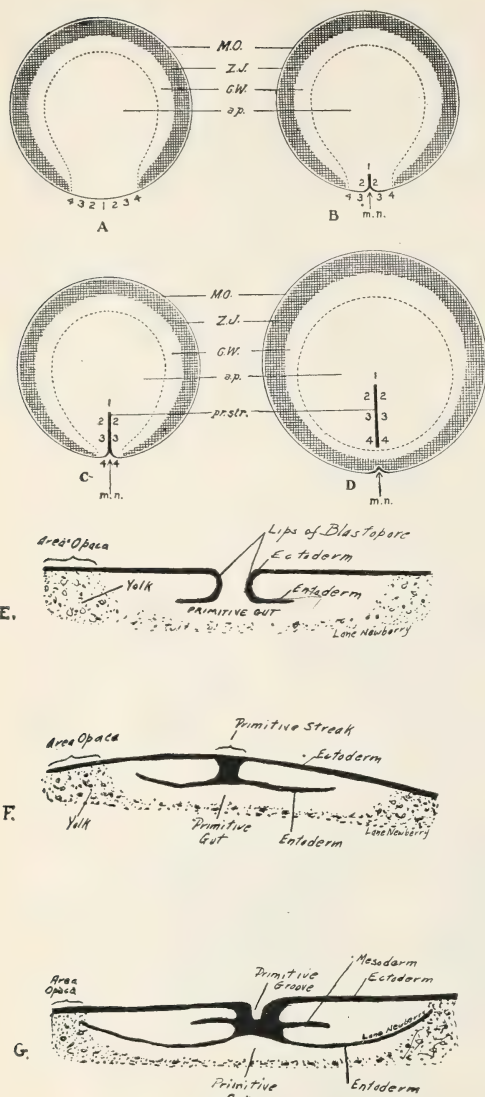


Fig. 261.

A to D. Diagrams illustrating the idea of confluence (concrescence) as applied to the chick. The central area bounded by the broken line represents the area pellucida; external to this is the area opaca, showing the germ wall (G. W.), zone of junction (Z. J.), and margin of over-growth (M. O.), m.n., Marginal notch.

E to G. Diagrammatic relations of the germ layers at the time the primitive streak is formed by concrescence of the blastoporal margins. E, section of stage B; F, section of stage D; G, section through blastoderm of a 16 hour chick embryo. (A to D from Lillie's "The Development of the Chick," by permission of Henry Holt & Co.)

forms are brought about by an inpushing of the outer layer of the blastula as though one were indenting a rubber ball. This forms a two walled (ectodermal and entodermal) cup with a cavity in the center, called a **gastrocoele**. The opening itself is known as the **blastopore** (Fig. 260).

In birds with a large amount of yolk, the blastula cannot indent completely into the blastocoele, due to the fact that the disc-shaped blastoderm is not a true hollow sphere. The very small blastocoele formed between the blastoderm and the yolk, allows but little infolding. The blastopore in the case of an indented sphere is relatively large. In the chick there is but a tiny blastocoele, while the blastopore is but a small crescent-shaped slit at the margin of the blastoderm (Fig. 251, C). This slit is to be thought of, however, as similar to the regular round opening in simpler forms, which has been pushed together by the yolk not yielding. The infolding entoderm is also naturally compressed and flattened by the tiny blastocoele into which it can grow. In fact, the lower layer of the infolding entoderm seems to be prevented from growing normally by the unyielding yolk, and so is broken and lies on the yolk as scattered cells. These scattered cells then shortly disappear so that the yolk itself forms the floor of the gastrocoele.

Figure 260 presents a diagrammatic scheme which makes it possible to see the general outlines of gastrulation in eggs with varying quantities of yolk.

The zone of junction, where the peripheral region of the blastoderm remains attached to the yolk, is called the **area opaca**, because when the blastoderm is removed from the yolk-surface for laboratory study, the yolk is so closely attached to this region that it adheres to the blastoderm and renders the area more opaque. The more central portion, which has no yolk attached, is more translucent and is, therefore, called the **area pellucida**.

The area opaca later differentiates into the following three more or less distinct zones (Fig. 261) :

(1) The **margin of overgrowth**, a peripheral zone where rapid proliferation pushes the cells out over the yolk without their adhering to it.

(2) The **zone of junction**, having an intermediate zone in which the deeper lying cells have no complete cell boundaries, so that they form a syncytium which blends (without a definite boundary) with the superficial layer of white yolk to which it adheres by many penetrating strands of cytoplasm.

(3) The **germ wall**, an inner zone made up of cells derived from the inner border of the zone of junction, which have acquired definite boundaries and become more or less free from the yolk. Numerous small yolk granules are usually found in the germ wall, due to the fact that these were contained in the cytoplasm when they were still connected with the yolk as cells of the zone of junction. It is the inner margin of the germ wall which separates the area opaca from the area pellucida.

When the chick embryo is ready for gastrulation, there is a thinning of the blastoderm at the caudal margin with a consequent freeing of the blastoderm at the caudal margin from the yolk (Fig. 259, D). In a surface view, the crescent shaped gap in the posterior quadrant of the zone of junction marks the separation of the blastoderm from the yolk (Fig. 259, A). The blastopore is that region where the blastoderm is free from yolk and where it is likewise very thin.

It will be remembered that cell proliferation is continuous throughout the entire blastoderm. The surface extent has now become much greater by a general spreading out of the peripheral margins over the yolk, but this extension, while taking place uniformly at the margins, varies at the blastopore. This being at the posterior free end of the blastoderm, the cells, as they proliferate, grow inward to form the entoderm. Once this differentiation has taken place, the part of the margin forming this entodermal portion takes no further part in the peripheral

expansion, although this entodermal part grows back toward the center of the blastoderm, leaving the blastopore region behind. The marginal region continues to grow and soon encloses it, so that by the time the blastopore comes to close, it lies within the recompleted circle of the germ wall (Fig. 259, C).

## CHAPTER II

### THE PRIMITIVE STREAK AND ORIGIN OF THE MESODERM

**A**LL that has been described so far has actually taken place before the egg is laid. The real beginnings of a distinguishable embryonic area may be said to start with the **primitive streak**. While there are various theories as to just how this thickened streak is formed, the most logical and intelligible is that it is a thickening formed by the two lips of the blastopore meeting and growing downward.

To make this clear, the student will remember that throughout this entire work, the blastula has been considered a hollow sphere composed of a single layer of cells, and the gastrula was this same hollow sphere after it had indented so as to form two layers. The opening where the indentation took place was called the blastopore.

In the chick-embryo we are to think of this blastula, however, not as a sphere, but as sausage-shaped, with the indentation taking place from about the center of the long axis to one end. Thus we do not have a round blastopore, but an **e'longated one**. And it is the closing of the lips along this elongated slit which forms the thickening called the primitive streak (Fig. 262). It is clearly seen at sixteen hours of incubation, not only as a thickening, but as an indentation—the **primitive groove**—with ridge-like thickenings, flanking each side and extending from the area opaca to almost the

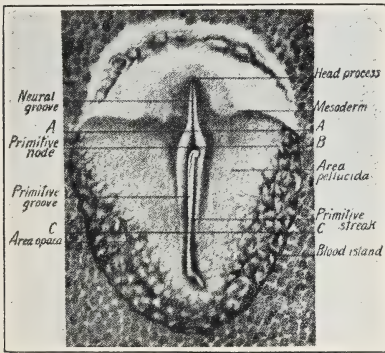


Fig. 262.

Dorsal view of 16 to 20 hour chick embryo showing primitive streak, primitive groove, primitive node, beginning of neural groove, blood-islands, and extent of mesoderm. (After Duval.)

center of the blastoderm. The part lying closest to the area opaca is the caudal end, and the direction of the streak forms the long axis of the embryo. At the cephalic end of the primitive groove there is a deepening, called the **primitive pit**, and directly anterior to this the two lips of the primitive folds meet in the midline to form a small rounded elevation, known as **Hensen's node**. This node serves as the region of demarcation separating the fast disappearing primitive streak from the notochord, which forms cephalad to it in the long axis of the embryonic area. The growth of the embryo is much greater headward than caudally or laterally, so that the antero-posterior axis becomes considerably elongated.

The lips of the blastopore form a region of rapid cell proliferation, though all the cells look quite alike. Nevertheless, it is from these rapidly proliferating cells that the various germ layers are derived.

Figure 263 shows an enlarged longitudinal, as well as a cross section of an early embryo. As the lips of the blastopore grow closer and closer together, they finally fuse, forming the primitive streak. Ectoderm and entoderm cannot be distinguished, but from the thickened approximation of the lips of the blastopore there is an inward growth of

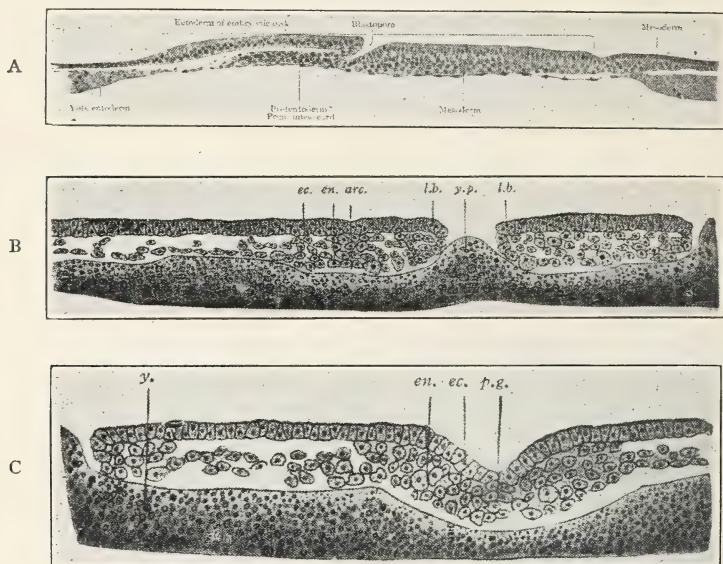


Fig. 263.

- A. From medial longitudinal section through embryonic disk of Chick. *Bonnet*.  
 B. From transverse section through Hensen's node—germ disk of chick of 2 to 6 hours' incubation. *Duval*. For lettering see Fig. C.  
 C. From transverse section through primitive groove—germ disk of chick of 2 to 6 hours' incubation. *Duval*. *arc.*, Archenteron; *ec.*, ectoderm; *en.*, entoderm; *lb.*, lip of blastopore; *y.*, yolk; *y.p.*, yolk plug.

a single layer of cells, now called entoderm, and from between these two layers some rather loosely arranged cells form a third layer, considered the primitive origin of what is later to be called **mesoderm**.

At the same time this mesodermal outgrowth appears, the dipping down of the outer layer occurs to form the **primitive groove**.

The three layers which have thus been established are very important because in all forms of animal life so far studied, there is a decided similarity in the origins and development of the various organ systems. Therefore, an understanding of the way the germ-layers and the organ systems arise, alone permits an understanding of the ever-increasing perplexities coming forth as these in turn develop further.

In our study of comparative anatomy we shall see why it is that

the nervous system as well as all outer coverings of the body are derived from the ectoderm; why the lining of both digestive and respiratory organs comes from the entoderm; and why the circulatory system as well as the blood, lymph, muscle, and connective tissue (except neuroglia) are derived from the mesoderm.

The primitive streak, relatively, seems to become pushed further and further tailward, but this is due to the greater growth in the cephalic region of the embryo. (Compare Figures 262 and 264.)

The entoderm spreads out as a very definite layer of cells, and merges peripherally with the inner margin of the germ wall, even overlapping it slightly. The little cavity between the yolk and this entodermal layer, which has been called the gastrocœle, will henceforth be known as the **archenteron** or **primitive gut** (Fig. 265). The student is not to look for a cavity in his sections, however, as the yolk in this region, by the very fact that it is separated from the entoderm and forms the floor of the primitive gut cavity, will not adhere to the embryo when it is removed for sectioning purposes.

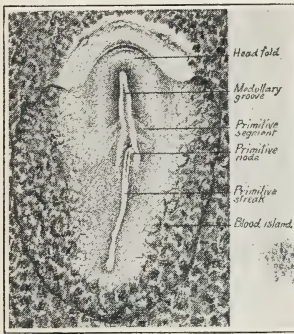


Fig. 264.

Surface view of a twenty-one hour chick embryo, in which the head-fold and first pair of primitive mesodermal segments are present. (After Duval.)

At eighteen hours of incubation the cell boundaries of the germ wall cannot usually be seen, though there are many nuclei and yolk granules, the latter in various stages of absorption. Because the nuclei of the germ wall arise by division of the nuclei of the cells lying at the margins of the expanding blastoderm, it is assumed they are instrumental in breaking up the yolk in advance of the arrival of the spreading entoderm about the yolk sphere.

At about twenty-two to twenty-three hours of incubation a pocket of entoderm can be seen in the anterior region by examining the whole mount, and focusing through the ectoderm. This is the first formation of a gut floor in addition to the yolk. It is the yolk which has been answering that purpose up to this moment. This pocket forms the **fore-gut**.

The mesoderm grows laterad and then extends cephalad, so that an area between the two cephalad growing portions of mesoderm is formed. This area is called the **proamnion** (Fig. 266, P) and is merely an open space, which must not be thought of as forming the later true amnion. It is to be noted primarily, because it permits a better study of just how the mesoderm grows in relation to it. It will be well to observe the difference in this space in eighteen and twenty-three hour embryos.

As the mesoderm begins its growth where it does, there is none of it in the midline except posterior to the primitive streak; but, immedi-

ately on each side of the midline, the mesoderm is quite thickened, thinning out as it extends toward each side. The dorsal mesodermic plates are to develop from these thickened portions of the mesoderm, and as they will then segment, they are called **segmental zones** of mesoderm. The first somites will appear cephalad to Hensen's node, extending caudally along each side of the primitive streak and becoming less and less distinct.

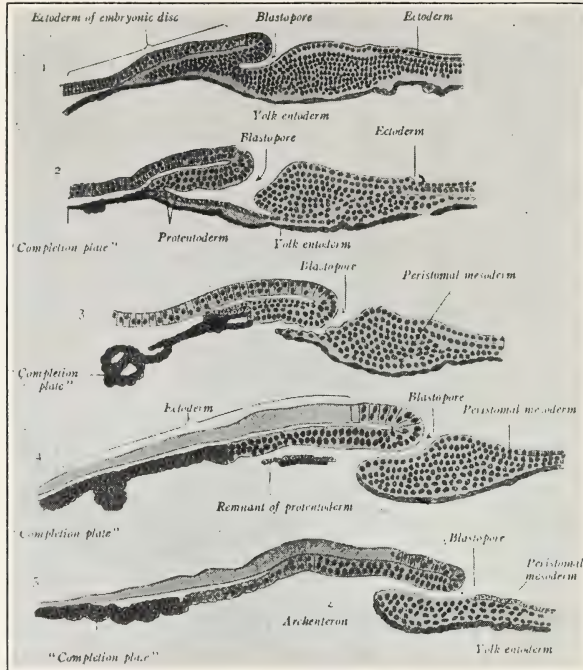


Fig. 265.

From medial vertical sections through embryonic disk of lizard, showing five successive stages in gastrulation (Wenckebach, Bonnet).

It is important to note here that the sheet-like layers of mesoderm, so characteristic in the mid-body region, do not extend to the head region of the embryo. The mesoderm of the head region develops from quite definitely organized layers immediately behind the future head. The reason that the mesoderm of the head is separate in origin from that of the remaining portion of the body, may be accounted for by the fact that the head is not segmented as is the mesoderm of the body-region.

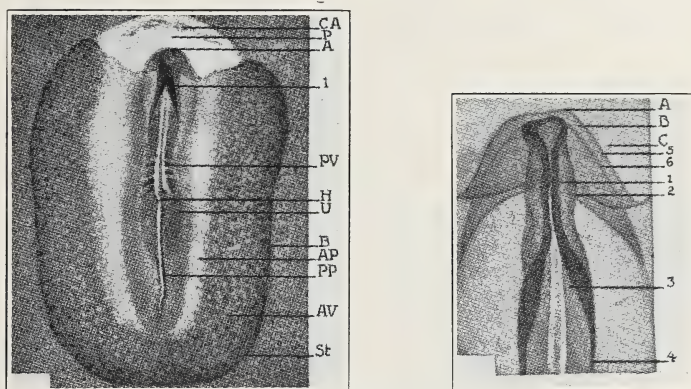
## THE NOTOCHORD

From the cephalic end of the primitive streak the rapidly proliferating cells extend in an anterior manner. In non-bird-like vertebrates,

the notochord extends from the region of the anterior lip of the blastopore, so it is assumed that this is also the case in birds.

If the student will think of assumptions and incidents of this kind, and note the manner in which hundreds of such assumptions and incidents must be gathered from all angles and from hundreds of experiments by hundreds of different investigators, to make such a study as embryology possible, he will obtain at least some slight appreciation of what **scientific investigation** means and what **scientific method** means.

In reading the literature on the subject, the student will note that probably most writers insist that the notochord develops from the entoderm, though there are those who believe that it comes from either of the other two layers, and some even that it comes from all three.



A Fig. 266. B

*A.*—Surface view of Embryo at the Twenty-third Hour of Incubation. *A.*, anterior limit of head; *AP.*, area pellucida; *AV.*, area vasculosa *B.*, border of mesoderm; *CA.*, yolk crescent; *H.*, Hensen's node; *P.*, proamnion; *PP.*, primitive streak; *PV.*, mesoblastic somites; *St.*, sinus terminalis bounding the vascular area; *U.*, unsegmented mesoderm; *1.*, region where the medullary folds have almost met to form the medullary canal.

*B.*—Anterior part of the preceding figure more highly magnified to show details. *A.*, ectoderm of anterior end of head; *B.*, mesenchyme; *C.*, subcephalic pocket: 1, region where the medullary folds will begin fusing to form medullary canal; 2, margin of the anterior intestinal portal; 3 and 4, posterior regions of medullary folds; 5, lateral limits of head region; 6, border of foregut. (From Duval.)

In all forms studied, however, the notochord is not seen to arise from any definite layer, but it arises either at the same time the mesoderm does (Fig. 267), or from the undifferentiated growth of cells about the closed blastopore which gives rise to both entoderm and mesoderm.

The notochord itself is a rod-shaped structure, circular in cross section, extending headward from Hensen's node.

## THE NEURAL PLATE

A thickening of the ectoderm at about eighteen hours' incubation causes a greater density along each side of the notochord. This denser area is several cells in thickness, and forms what is called the neural or

**medullary plate.** From Hensen's node caudad, the lateral portions of the medullary plates diverge into thickenings on each side of the primitive streak.

At twenty-one to twenty-two hours the outer portions of the neural plate bend dorsally toward the midline and form the **neural** or **medullary groove**; the ridges thus formed are called the **neural** or **medullary folds** (Fig. 266, B). This is the first differentiation of the nervous system.

After this period of incubation the denser portion which has formed by the cell differentiation mentioned above, is called the **embryonal area**, and the outer peripheral region of the blastoderm is called the **extra-embryonic area**, because from this extra-embryonic region arise those structures which are not part and parcel of the embryo itself, but serve as protective and nutritive layers.

At this period the **anlage** of the head appears as a rounded elevation with a definite crescent-shaped head-fold, the first definite boundary of the growing embryo.

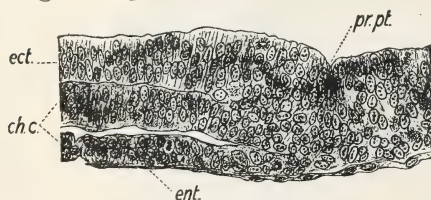


Fig. 267.

Sagittal section through region of primitive node and caudal end of choral canal of guinea pig (13½ days after fertilization) to show beginning of notochordal cells and ectodermal cells in one layer. *Ect.*, ectoderm; *ent.*, entoderm; *ch.c.*, choral canal, dorsal and ventral wall closing lumen; *pr.pt.*, primitive pit. (After Huber in The Anatomical Record, April 20, 1918.)

It is well at this point to know what is to become of the mesoderm, so as to have several landmarks which will stand us in good stead.

In the earthworm, it will be recalled, the entire animal is segmented, that is, composed of **metameres**; while in the frog, segmentation shows itself primarily in the spinal column.

In both earthworm and frog the segments are composed of an outer layer of ectoderm, an inner layer of entoderm, and a middle layer of mesoderm.

When one speaks of metameres, one always means segments lying **one behind the other**, but now we must think of a sort of segmentation also in each metamere, one below the other (Fig. 268). In fact, this we must do if we are to understand that which follows.

Figure 268 shows a combination transverse and longitudinal arrangement of metameres with the mesoderm divided into an outer (somatopleure) and an inner (splanchnopleure) layer, and the segments also divided horizontally.

The more dorsal portion of the horizontal divisions is called an **epimere**, the mid-portion a **mesomere** (which is the beginning of the excretory system), and the more ventral portion is known as a **hypomere**. The whole metamere is called a **mesomeric somite**.

In vertebrates, as we have seen, segmentation is observable pri-

marily in the region of the spinal column. Therefore, in the study of vertebrates, such as the chick, we shall find that, while segmentation begins along the future spinal region, only the more dorsal portion of the mesoderm is segmented, and that only partially. The epimeres alone, that is, the paired parts lying at the side of the notochord, are truly segmented, though the opening in them, the **epicoele**, shortly disappears. The mesomeres with their mesocoels develop into the excretory system, and the hypomeres, which have not segmented, but whose opening, the **hypocoele**, is continuous throughout the entire region where there has been any segmentation, is now to be known as the **coelom**, or **body cavity**, into which the internal organs are to grow.

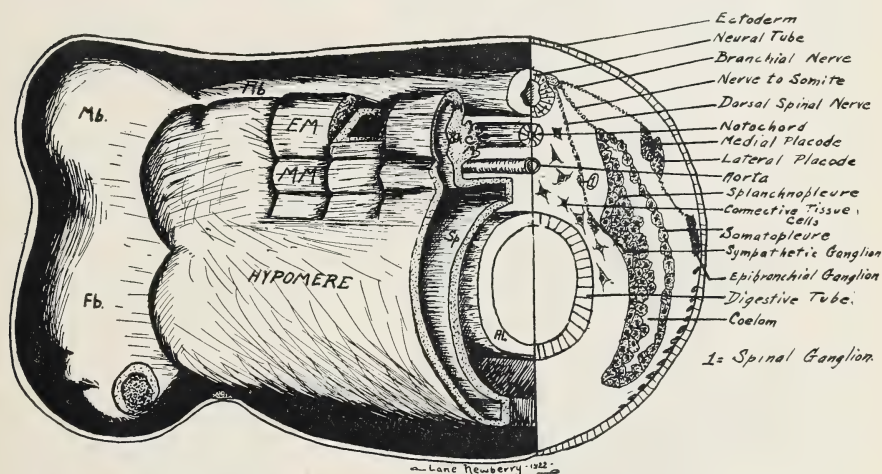


Fig. 268.

Stereogram showing the segmentation of the mesothelium. The dorsal and ventral walls of the coelom later fuse to form the dorsal and ventral mesenteries. *Al*, alimentary canal; *EM*, epimere; *Fb*, forebrain; *Hb*, hindbrain; *M*, (under *Sk.c.*), myotome; *Mb*, midbrain; *MM*, mesomere; *sk.c.*, sclerotome; *Sp*, splanchnic layer of the mesoderm (splanchnopleure). (Modified from Kingsley.)

It is to be remembered that epimere, mesomere, and hypomere are composed of mesoderm only.

As the mesoderm begins to grow laterad and ventrad, and while it is yet unsplit into an outer and inner layer, the thickened portion lying on each side of the neural groove is called the **vertebral plate**, and the more distal portion, the **lateral plate**.

The outer layer of the lateral plate, after it splits into two sheets, is called **somatic mesoderm** (and after connecting with the ectoderm, the **somatopleure**) while the inner layer, the **splanchnic mesoderm**, connects with the entoderm and is known as the **splanchnopleure** (Fig. 268).

In the head region, the cells of the vertebral plate scatter and combine with cells which are continually being budded off from the walls of the fore-gut to form the **mesenchyme** of the head region (Fig. 269). It will thus be seen that mesenchyme is made up of a combination of

cells from both mesoderm and entoderm, and even of ectoderm, for, scattered cells later join from the ectoderm of the head region.

The somites begin forming in the region of the more anterior end of the primitive streak, the first one to develop remaining the more anterior. The first four pair of somites take part in the development of the hinder part of the head region of the embryo.

A further important factor to remember at this point is that seg-

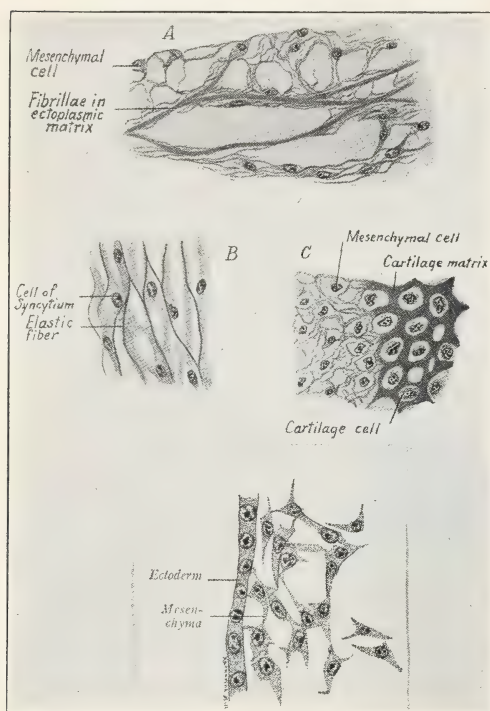


Fig. 269.

Figures showing the differentiation of the supporting tissues (after Mall). *A*, white fibers forming in the dermis of a 5 cm. pig embryo; *B*, elastic fibers forming in the syncytium of the umbilical cord from a 7 cm. embryo; *C*, developing cartilage from the occipital bone of a 20 mm. pig embryo. Mesenchyma from the head of a thirty-six hour chick embryo.

mentation is fundamental, and that consequently any structures in the body, which show segmentation, only follow out some plan of the original segmentation. This is of value in tracing the growth of various body-parts, such as muscles, for instance, in that the nerve supply, which we shall shortly see is also of segmental origin, definitely tells us where a muscle springs from, because nerves always follow muscles, and not vice versa.

The **somatopleure**, **splanchnopleure**, and **coelom** become separated into **embryonic** and **extra-embryonic** regions later, although, at this early stage of which we are writing, they form continuous structures which extend laterally out from the germ wall, and anteriorly into the head region.

The following structures are developed from the embryonic portion:

- body-wall,
- gut-wall,
- vascular organs,
- pericardial cavity,
- pleural cavity,
- peritoneal cavity.

From the extra-embryonic portion the following are developed: embryonic membranes and appendages, extra-embryonic portions of the vascular system, extra-embryonic coelom (exocoelom).

Probably the most understandable method of making much of what has been said clear, is to use Professor Reese's method of illustration:

"An understanding of the way in which the embryo becomes folded off from the rest of the egg, may perhaps be obtained in the following way: Cut out four circles of cloth, say 75 cm. in diameter, of three different colors. Put the two circles that are of the same color together, and then put these two circles between the other two.

"Let these superimposed circles represent a greatly enlarged blastoderm that has been removed from the yolk to which it was originally

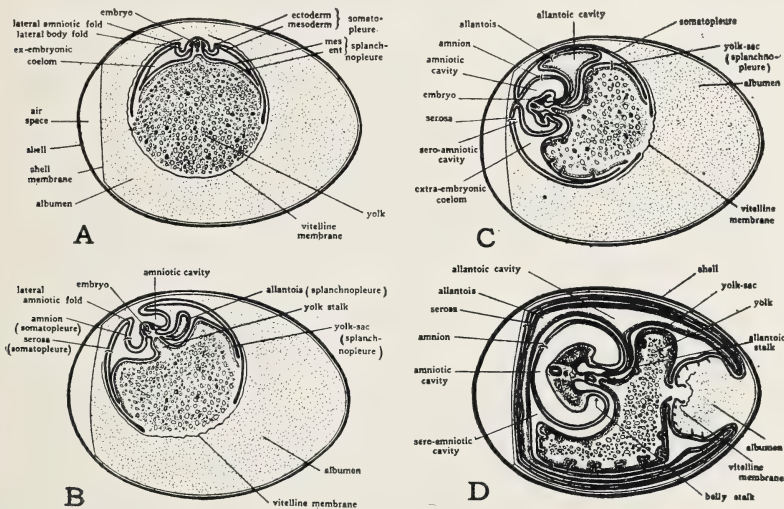


Fig. 270.

Schematic diagrams showing the extra-embryonic membranes of the chick. The egg is cut longitudinally while the embryo (which lies at almost right angles to the egg), is cut transversely. A, embryo at about 48 hours; B, same at about 72 hours; C, same at about five days; D, same at about fourteen days. (After Duval.)

attached. The upper layer of cloth will represent the ectoblast, the bottom layer will represent the entoblast, and the two similarly colored layers in the middle will represent the two layers of the mesoblast after their separation.

"As the yolk takes no actual part in the formation of the embryo other than as a supply of the food for the growth of the constantly enlarging chick, it may be omitted from our model.

"Now spread the cloth-blastoderm upon a table and place under its center a small object, such as a bottle. If now, the fingers of one hand be pushed under one end of the bottle, carrying, of course, the three

germ layers with them, we shall have represented the formation of the head fold. By pushing under the cloth at the other end of the bottle, in the same way, we may represent the formation of the tail fold; and in a like manner the lateral folds may be formed. If these folds, the head, tail, and lateral be pushed under far enough, they will meet under the center of the bottle, and we shall have the bottle, with its surrounding layers of cloth, connected with the rest of the model by only a sort of stalk, which is hollow and composed of the three layers of cloth. The bottle is used simply to give a solid object around which the folding may be more easily done, but we are to consider the space occupied by the bottle as an **empty** space.

"We have now represented what is sometimes called the **embryo-sac**, or simply the embryo, in contradistinction to the **yolk-sac**, or simply the yolk. The embryo remains connected with the yolk throughout the period of incubation by the **yolk** or **somatic-stalk**, and as the embryo increases in size, the yolk-sac is, by absorption, constantly diminished. The space occupied by the bottle, in our model, represents the digestive tract of the chick, and is lined, as will be seen by examination of the model, by the lower germ layer, or entoblast. The body cavity would be difficult to represent in the cloth model, but it can be imagined to exist as the narrow space between the two layers of similarly colored cloth which we have just called the mesoblast.

"The formation of the amnion may be represented in our model by lifting up with the fingers a small fold of the upper and second layers of cloth, and pulling these two layers back over the head end of the embryo, this fold will correspond to the head fold of the amnion. Similar folds might be lifted up at the posterior end and at the sides of the embryo model, to represent the tail and lateral folds of the amnion. The way in which these folds fuse together will be explained later."

The allantois cannot be explained from the model, but can be understood by studying Figure 270. It arises as a thin-walled pouch from the posterior end of the digestive tract, and as it increases in size, it extends around the upper side of the embryo, between the inner and outer layers of the amnion.

Both amnion and allantois are thrown off at hatching, so take no permanent part in the actual embryo.

## CHAPTER III

### THE FOUR TO SIX SOMITE STAGE

(About Twenty-four Hours)

AS the embryo is already well on its way in development at the time the egg is laid, and as it has been shown that the extent of development varies considerably on account of the retention of the egg in the hen for an extra twelve to sixteen hours if it is not ready for laying sufficiently early in the day, the formation of the block-like portions of mesoderm—the somites—becomes the more accurate measurement of the age of an embryo. Chicks with the same number of somites do not usually vary much among themselves in general, though individual parts often do; while chicks, which have been incubated for the same number of hours, vary considerably in all parts.

The twenty-four hour stage (four to six somites), (compare Figs. 264 and 266), is of great importance, for it is during this very early period of the chick's life that the interesting and important differentiating processes are noted. Up to the time the first four somites form, the entire growth of the embryo from Hensen's node cephalad, has been a formation of the head-region only.

There has been some question in the past as to whether or not additional somites are formed anterior to the first ones thus laid down. Professor Patterson performed an interesting experiment which seems to warrant our saying that such is not the case.

Professor Patterson incubated six eggs up to the one somite formation period, and then with the most aseptic precautions, opened the eggs and marked the first somite by injuring it with an electric needle, or inserting a minute glass pin therein. The shell was then again closed by a small piece of egg-shell, and the eggs again incubated for varying number of hours before being reopened. No new somites appeared anterior to the injured one.

In the study of whole mounts under the microscope, it must be remembered that reflected light, coming up from below the object, shows different densities as darker or lighter areas. Any portions of the embryo, which have become thickened or folded over, will, therefore, appear extremely dark and be thus distinguished from the thinner and lighter areas.

At the end of about twenty-four hours we then have:

1. Three definite germ layers. (Fig. 271.)
2. Four to five somites, forming in the vertebral plates, which vertebral plates have separated from the lateral plates.
3. The mesoderm divided into a somatic and a splanchnic layer.

4. The neural groove almost but not quite closed.
5. A clearly outlined fore-gut and mid-gut.
6. Clearly defined head-folds, marking the anterior limit of the embryo.
7. A definite notochord, extending from the anterior end of the primitive streak to what is to become the mid-brain.
8. The pellucid area is more or less pear-shaped, and the vascular area is seen as an inner zone of the area opaca.
9. The primitive streak is rapidly becoming relatively shorter and is soon to disappear, the cells of which it is composed probably becoming rearranged to form other structures.

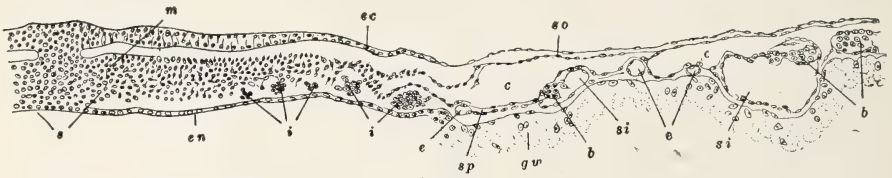


Fig. 271.

Transverse section through the primitive streak of a chick with six pairs of mesodermal somites (about twenty-four hours), showing the formation of the blood-vessels and blood. The section extends from the mid-line, nearly half across the area vasculosa. *b*, Blood cells; *c*, coelomic spaces; *e*, empty endothelial tubes; *ec*, ectoderm; *en*, endoderm; *gv*, germ wall; *i*, solid blood island; *m*, axial mesoderm; *s*, primitive streak; *si*, vascular sinuses of area vasculosa; *so*, somatic mesoderm; *sp*, splanchnic mesoderm. (After Rückert.)

From the twenty-fourth hour on, the texture of the embryo becomes firmer, and, whereas, it is difficult to remove an eighteen-hour embryo without tearing. The twenty-four hour embryo can easily be removed. All outlines also become clearer.

The anterior part of the embryonal area has thickened, and is slightly lifted above the remaining blastoderm, as shown by the crescent-shaped anterior boundary (Fig. 266, B). The embryo grows forward over this crescent-shaped fold which thus comes to lie under the embryo and forms a little pocket between the embryo and the fold called the **subcephalic pocket**.

The neural folds now unite in the region of the future mid-brain, closing rapidly posteriorly, and slowly anteriorly. The closed portion is called the **neural tube**. The most anterior portion, where the neural tube will close, is known as the **neuropore**, which is the region of what is later to become the **lamina terminalis**. This lamina terminalis is usually regarded as the **morphologically anterior limit** of the brain. **Topographically**, however, this is not the case, for the fore-brain grows forward and then bends back downward in front of the fore-gut, the whole formation becoming bent like a shepherd's crook, so that the morphologically anterior end comes to lie on its antero-ventral aspect.

The neural folds have a somewhat flattened crest, and these fold inward, forming a vertical contact. The neural tube is thus formed by

the fusion of the lower or inner margins of these surfaces, the upper ones again forming a continuous ectoderm, so that the neural tube becomes entirely separated from it. The cells lying between this ectodermal and lower margin, and which have been derived approximately from the apices of the neural ridges, become the **neural crests** (Fig. 272). These crests do not fuse in the midline, but remain as a pair of longitudinal bands along the dorsal-lateral surfaces of the neural tube, and are the rudiments of the **ganglia of the cranial and spinal nerves**. They are not uniformly developed, and appear much clearer in some sections than in others.

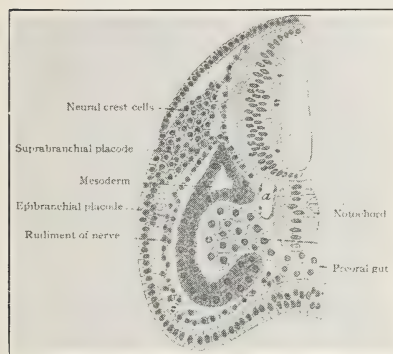


Fig. 272.

Transverse section through the head of a 7 day *Ammocoetes* in the region of the trigeminal ganglion. (After von Kupffer.)

blood vessel forms, known as the **sinus terminalis** (Fig. 284, C). Beyond this sinus terminalis, all the remaining area opaca consists of ectoderm and entoderm, and extends around the yolk. It is then called the **area vitellina**.

The compact cell masses forming these blood-islands have been formed throughout the deeper portion of the germ wall, becoming covered superficially with a deep layer of scattered germ wall cells. This superficial layer comes to be known as coelomic "**mesoderm**."

This superficial layer and the blood islands become continuous very early with the mesoderm of the pellucid area derived from the primitive streak (Fig. 273). The blood islands become hollowed out, forming **lacunae**. The cells, which have formed the blood islands, become both the blood-vessel walls and the blood cells. The lacunae then anastomose, forming a complete network extending to meet the vascular structure of the pellucid area and later of the embryo.

The cellular portion of the germ wall, which remains after the coelomic "**mesoderm**" and the blood islands have differentiated, forms the rudiment of the yolk-sac entoderm, to be described later.

So soon as the extra-embryonic coelom forms, dividing the meso-

derm into somatic and splanchnic layers, the blood vessels remain associated with the splanchnic layer.

Just as the somites are beginning to form, blood vessels will be found at the margin of the pellucid area, beginning to grow toward the embryo. Only the tubular vessels develop in the area pellucida; the blood islands, as already noted, develop in the area opaca. This means that the cellular, or **corpuscular, elements** of the blood arise in the posterior region of the area opaca.

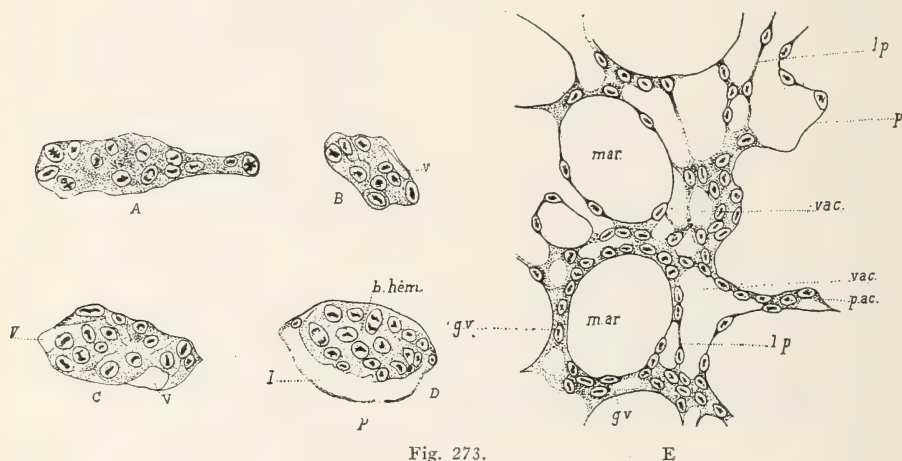


Fig. 273.

Beginning of the vascular system in the chick embryo. *A*, complete blood island; *B* and *C*, beginning of vacuole formation; *D*, vacuoles becoming confluent to form the lumen of the blood vessel. *b.hem.*, primitive red blood cells; *l*, lumen; *p*, vessel-wall; *v*, vacuole or lacunae. (After Uskow). *E*. A portion of the vascular net work destined to become the aorta in the chick embryo. *gv*, primitive blood forming cells; *lp*, cytoplasmic lamina persisting in the lumen of the blood vessel that has formed; *mar*, blood vessels; *p*, vessel wall; *p.ac.*, point of enlargement of network; *vac.*, vacuoles. (From Vialleton.)

Professor Rückert has worked out the arrangement of the blood vessels (Fig. 284). He says the vessels in the area pellucida are formed by a rearrangement of small groups of cells in the splanchnic mesoderm of the area. First, short sections of tubular vessels are formed, which then connect with the more peripheral vessels of the opaque area, thus forming a continuous vascular network extending toward the embryo and finally reaching it at about the time six pairs of somites are formed.

Soon after this, vessels appear in the embryo itself, the first being the paired **dorsal aorta** in the body region. These are regarded as merely straightened axial margins of the vascular network of the area pellucida. They diverge widely posteriorly, passing as the **vitelline arteries** into the general vascular network. Anteriorly they are prolonged forward to the heart region where they connect with a pair of vessels differentiated in the mesenchyme of the head.

It will be remembered that the coelom is really paired, and extends downward ventrally on both sides until at a later period it meets in the

ventral midline and fuses to form the one cavity which it later becomes in all vertebrates. The crescent-shaped line where fore-gut and mid-gut meet, is called the **anterior intestinal portal** (Fig. 266, B).

It is in the region of the anterior intestinal portal that the coelomic chambers on both sides show a marked enlargement. The enlargement of each side extends mesiad toward the other, and finally both break through into each other ventral to the fore-gut, to form the pericardial cavity. These enlarged regions are called the **amnio-cardiac vesicles** (Fig. 274) in their early stages; however, it is better to remember what

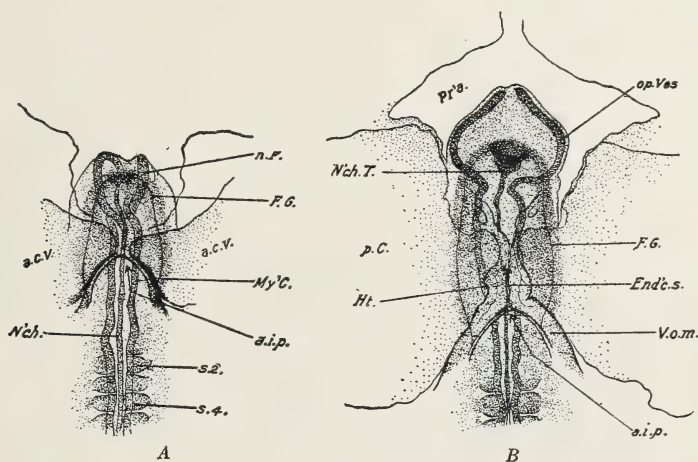


Fig. 274.

Ventral views of the head ends of chick embryos. *A.* Embryo with five pairs of somites (about twenty-three hours). *B.* Embryo with seven pairs of somites (about twenty-five hours). *a.c.v.*, Amnio-cardiac vesicle; *a. i. p.*, anterior intestinal portal; *End'c.s.*, endocardial septum; *FG.*, fore-gut; *Ht.*, heart; *My'C.*, myocardium; *N'ch.*, notochord; *N'ch.T.*, anterior tip of notochord; *n.f.*, neural fold, *op. Ves.*, optic vesicle; *p.C.*, parietal cavity (coelomic); *Pr'a.*, proamnion; *s.2.*, *s.4.*, second and fourth mesodermal somites; *V.o.m.*, omphalo-mesenteric vein. (From Lillie's "Development of the Chick" by permission of Henry Holt & Co., Publishers.)

they are to become, and think of them as the **pericardial region of the coelom**.

The splanchnic mesoderm is thickened at the point where it lies closely applied to the entoderm at the lateral margins of the portal. It is from these thickened areas that the paired primordia of the heart will arise later.

It will thus be noted that the heart develops from the ventral and not the dorsal aspect.

The amnio-cardiac vesicles also become vascularized quite like the rest of the pellucid area, and a pair of **ventral aortae** are formed beneath the fore-gut. Immediately posterior to the anterior intestinal portal these vessels diverge, passing into the vascular network as the rudiments of the vitelline veins.

## CHAPTER IV

### THE FIRST HALF OF THE SECOND DAY

(Twenty-four to Thirty-six Hours)

IT IS well at this point to continue with the vascular system, and to give a connected account of how the heart and the various blood vessels are formed.

The paired primordia of the heart, already mentioned, grow mesiad and fuse to form a thin-walled tube which becomes the **endothelial lining** of the heart (Fig. 275). The muscular walls of the heart are formed by the addition of an external layer of mesoderm. This is understood the better by noting that the splanchnic mesoderm on each side forms a fold around the endothelial rudiment and fuses both dorsally and ventrally

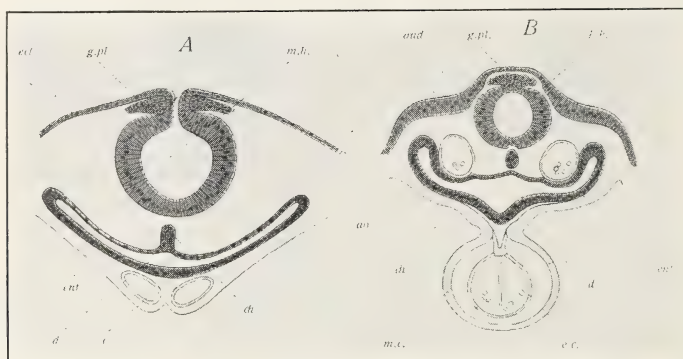


Fig. 275.

Cross section of *A*, through head of 2 day chick embryo in the region of the mid brain. *B*, through posterior region of head at the end of 3 days. *ao*, aorta; *aud*, otic anlage; *c*, heart anlage; *ch*, notochord; *d*, fore-gut; *ec*, endocardium; *ect*, ectoderm; *ent*, entoderm; *g.pl.*, neural crest; *h.h.*, hindbrain; *m.c.*, myocardium; *m.n.*, midbrain. (After Marshall.)

in the midline. For a very short period this fusion remains on the dorsal aspect, being called the **dorsal mesocardium**. The ventral fusion forms the **ventral mesocardium**. The ventral mesocardium breaks away almost immediately, the dorsal mesocardium remaining for a longer time, but then it also disappears with the exception of the portion at the anterior and posterior extremities of the heart. The heart is now a short median tube made up of endothelial and rudimentary muscular layers, suspended in a cavity, later to be called the **pericardial cavity**. Anteriorly, the heart-tube is continuous with a short pair of vessels extending into the head-fold—the ventral aortae already mentioned.

Posteriorly the heart-tube is continuous with the vitelline or omphalomesenteric veins (Fig. 276).

The two vessels of the heart (Fig. 283) come in contact so as to form the letter V, with the point of the V toward the head of the embryo. The arms continue fusing until a Y-shaped stem has been developed, with the stem toward the head.

Although the two tubes unite in the manner just mentioned, their cavities remain distinct for a short time, the endothelial lining forming two distinct cavities until a short time after the muscular walls have fused. The muscular walls themselves are not complete on the dorsal side for a short time, but as soon as the tubes have thoroughly fused, the walls also complete their function.

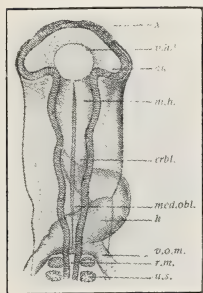


Fig. 276.

Anterior region of 2½ day chick embryo. *au*, optic vesicle; *crbl*, cerebellum; *h*, heart; *m.h.*, vesicle of midbrain; *med.obl.*, medulla oblongata; *r.m.*, spinal cord; *u.s.*, primitive segment; *v.h.*, primary vesicle of the forebrain; *v.o.m.*, omphalo-mesenteric vein; *x*, anterior wall of primitive forebrain which later expands into the cerebrum. (After von Mihalkovics.)

It is the stem of the Y which forms the true heart, the two arms being continuous with the large vitelline veins which carry blood to the heart from the vascular area. The caudal end of the heart is then said to be venous, while the cephalic end is known as the arterial end.

At the thirty hour period the heart is a short straight tube attached to the ventral wall of the fore-gut or pharynx. The point where the vitelline veins diverge is at the hindermost angle of the head-fold. As the head-fold is pushed farther and farther back, the straight portion of the Y is lengthened, but as the tubular heart seems to grow more rapidly than does the place to which it is attached, it is bent into a loop, with its convexity toward the right side of the embryo. This looping is made possible by the fact that the heart has by this time lost all connection with the wall of the fore-gut and remains attached only at both ends.

It is even before this period that the heart begins to beat, the pulsations beginning at the venous end and passing to the arterial end. In fact, the beating began before any muscular differentiation could be observed in the heart region.

The cephalic end of the heart is known as the **bulbus arteriosus**. The bulbus branches immediately into two narrow vessels, the **aortic arches**, one passing upward on each side of the digestive tract to the dorsal side of the embryo and then running tailward as the paired **dorsal aortae** (Fig. 277). These vessels lie close to the notochord under the somites, and extend as separate vessels almost to the tail, where a larger branch than the vessel itself is given off from each. These two larger branches are the **vitelline arteries**, which carry the blood from the heart back to the vascular area.

## THE DIFFERENTIATION OF THE BRAIN REGION

At twenty-seven hours, the more cephalic end of the neural tube has become considerably enlarged as compared with the more caudal portion. The walls are thicker and the lumen larger. This portion is to become the brain proper, and the portion in which the lumen has not enlarged becomes the spinal cord. A picture of the brain at this time (Figs. 278 and 282) will show three **primary vesicles** or lumen-enlarge-

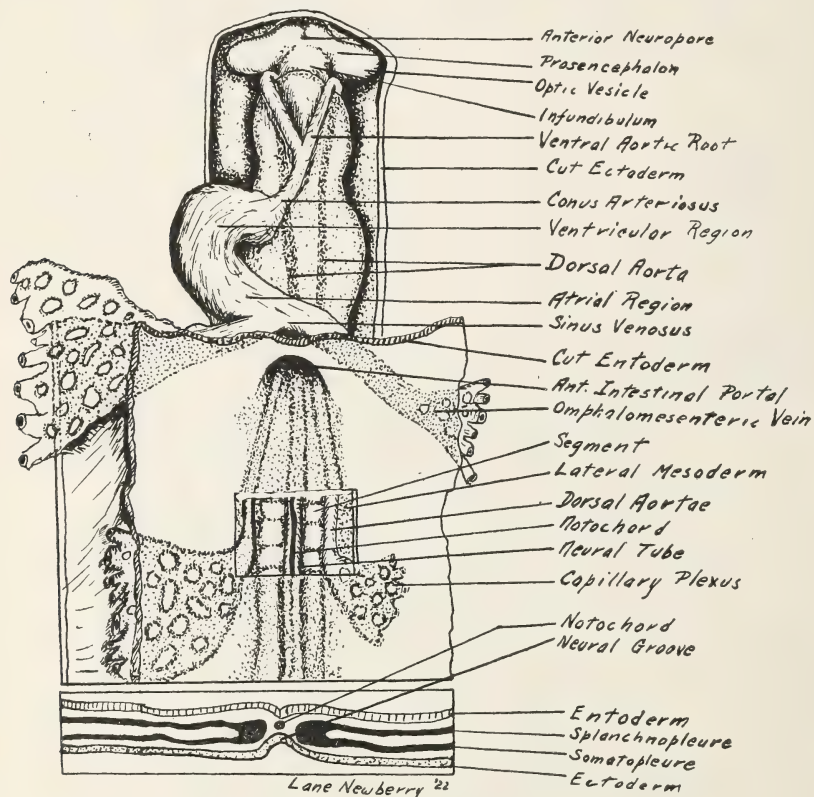


Fig. 277.

Diagrammatic ventral view of a 35-36 hour chick embryo. Compare with Figures 279 and 280. (Modified from Prentiss.)

ments together with what these three vesicles later become. The most anterior of the three primary vesicles is known as the **fore-brain** or **prosencephalon**. The mid portion is called the **mid-brain**, or **mesencephalon**, while the most posterior vesicle forms the **hind-brain**, or **rhombencephalon**. The rhombencephalon is continuous with the spinal cord.

As all further developments of the brain arise from these three primary regions, it is of the utmost importance that these primary regions be grasped fully.

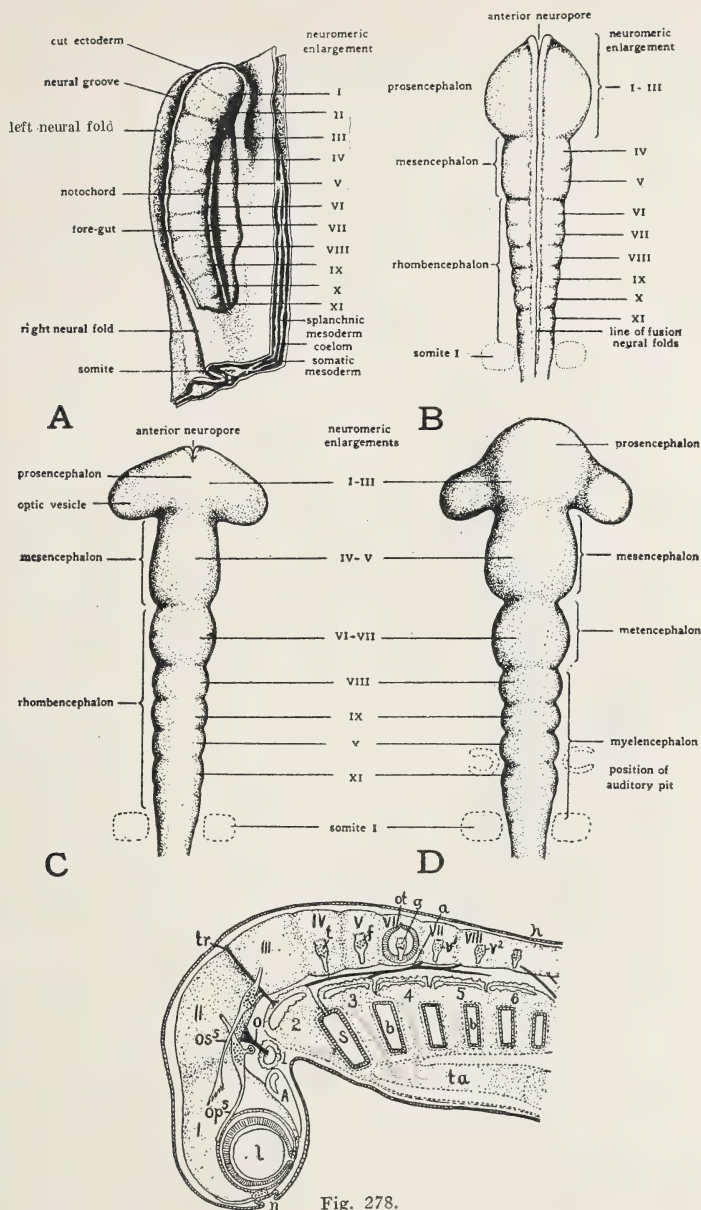


Fig. 278.

Diagrams showing neuromeres in brain region of the neural tube. *A*, lateral view of neuralplate of 24 hour chick embryo. *B*, dorsal view of brain from a 26-27 hour (7 somite) chick embryo. *C*, dorsal view of brain from a 30 somite (10 somite) chick embryo. *D*, dorsal view of brain from a 36 hour (14 somite) chick embryo. *E*, diagram of the segments (neuromeres, myotomes, etc.) of the head in longitudinal section. *A*, anterior myotome; *a*, abducens nerve; *b*, branchial clefts; *f*, facial nerve; *g*, glossopharyngeal nerve; *h*, hypoglossal nerve; *l*, lens surrounded by layers of eye; *n*, nasal pit with the terminal nerve nearby; *o*, oculomotor nerve; *op*<sup>s</sup>, ophthalmicus profundus part of fifth nerve; *os*<sup>s</sup>, ophthalmicus superficialis part of the fifth nerve; *ot*, otocyst; *s*, spiracular cleft; *t*, trigeminal nerve; *ta*, truncus arteriosus; *tr*, trochlear nerve; I-VIII, neuromeres; 1-6 myotomes. (*A-D*, from Patten after Hill, *E*, from Kingsley after Neal.)

From the lateral walls of the prosencephalon the primary **optic vesicles** push out as a pair of rounded pockets, the lumen of each being directly continuous with that of the fore-brain.

The notochord extends as far as the **infundibulum** (Fig. 282, A), (a depression in the floor of the fore-brain), so that all regions of the brain lying anterior to it are called **pre-chordal**, while the rhombencephalon, mesencephalon, and the part of the prosencephalon posterior to the infundibulum, which lie dorsal to the notochord, are called **epi-chordal**.

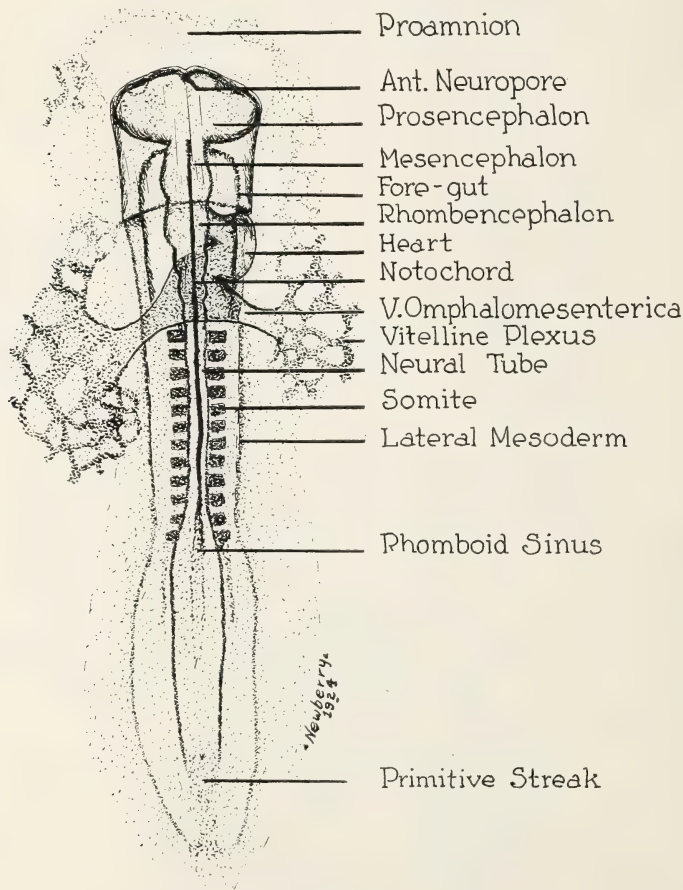


Fig. 279.

33 hour chick embryo (12 somites).

As has been noted previously, the most anterior region, where the neural tube closes, is called the **neuropore**. The neuropore is still open at this time and remains so, although gradually becoming smaller until after the thirty-third hour period, but even then, there is a scar-like

fissure. As we know of no structure arising from the neuropore, it is important only as a sort of landmark in describing the location of brain structures.

At this time the neural tube is closed back as far as the somites, and it is of nearly uniform diameter, although, posterior to the last formed somites, the neural tube is still open, and the neural folds can be seen to diverge on either side of Hensen's node (Fig. 279), leaving an opening rhomboidal in shape. This is the **rhomboid sinus**.

In lower forms, there is an opening from the neural canal into the digestive tract, known as the **neurenteric canal**, or **posterior neuropore**, at the point where the blastopore does not close until after it is surrounded by the neural folds. In the chick the **primitive pit** represents this region of the neurenteric canal.

Shortly after the twenty-seventh hour period, and as soon as the caudal end of the chick can be definitely outlined, the primitive streak disappears entirely.

### LENGTHENING OF THE FORE-GUT

The crescent-shaped margin of the anterior intestinal portal grows more and more caudad, first because the margin from each side grows toward the midline to fuse with the other side, thus lengthening the fore-gut by adding to its floor, and pushing the crescentic margin caudad; and second, all structures anterior to the anterior intestinal portal are elongating so rapidly that the portal is bound to lie further and further caudad from the cephalic end of the embryo.

These two processes together cause the space between the sub-cephalic pocket and the margin of the anterior intestinal portal to become elongated, and it is in this enlarging space that the pericardial portions of the coelom extend, and in which the heart comes to lie.

## CHAPTER V

### THE SECOND HALF OF THE SECOND DAY

(Thirty-six to Forty-eight Hours)

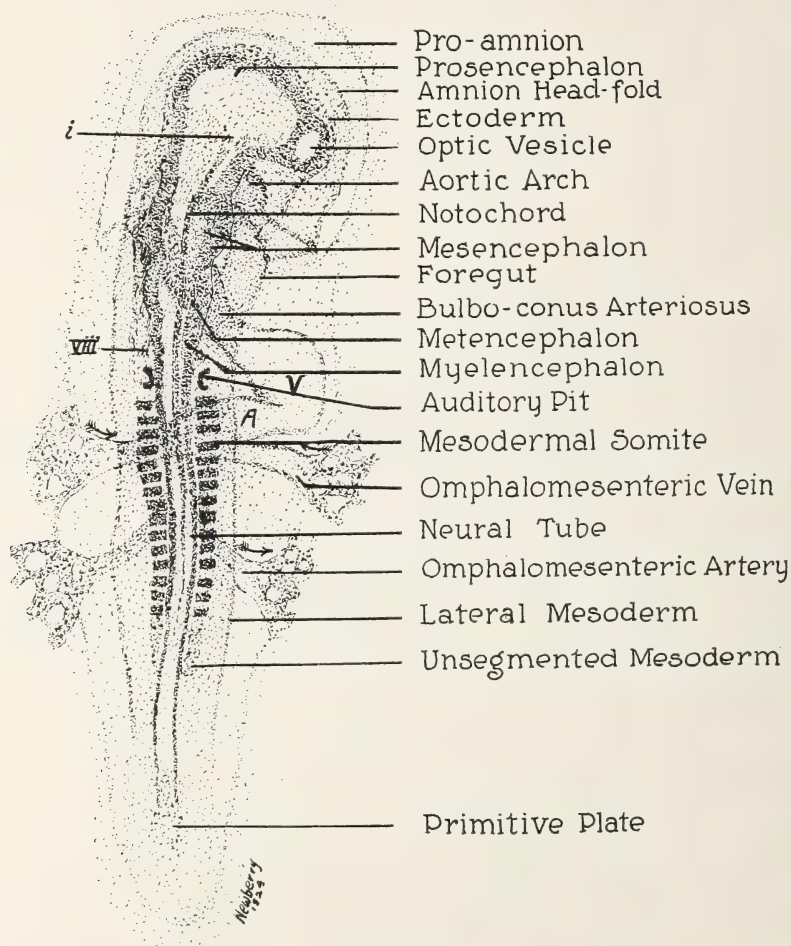
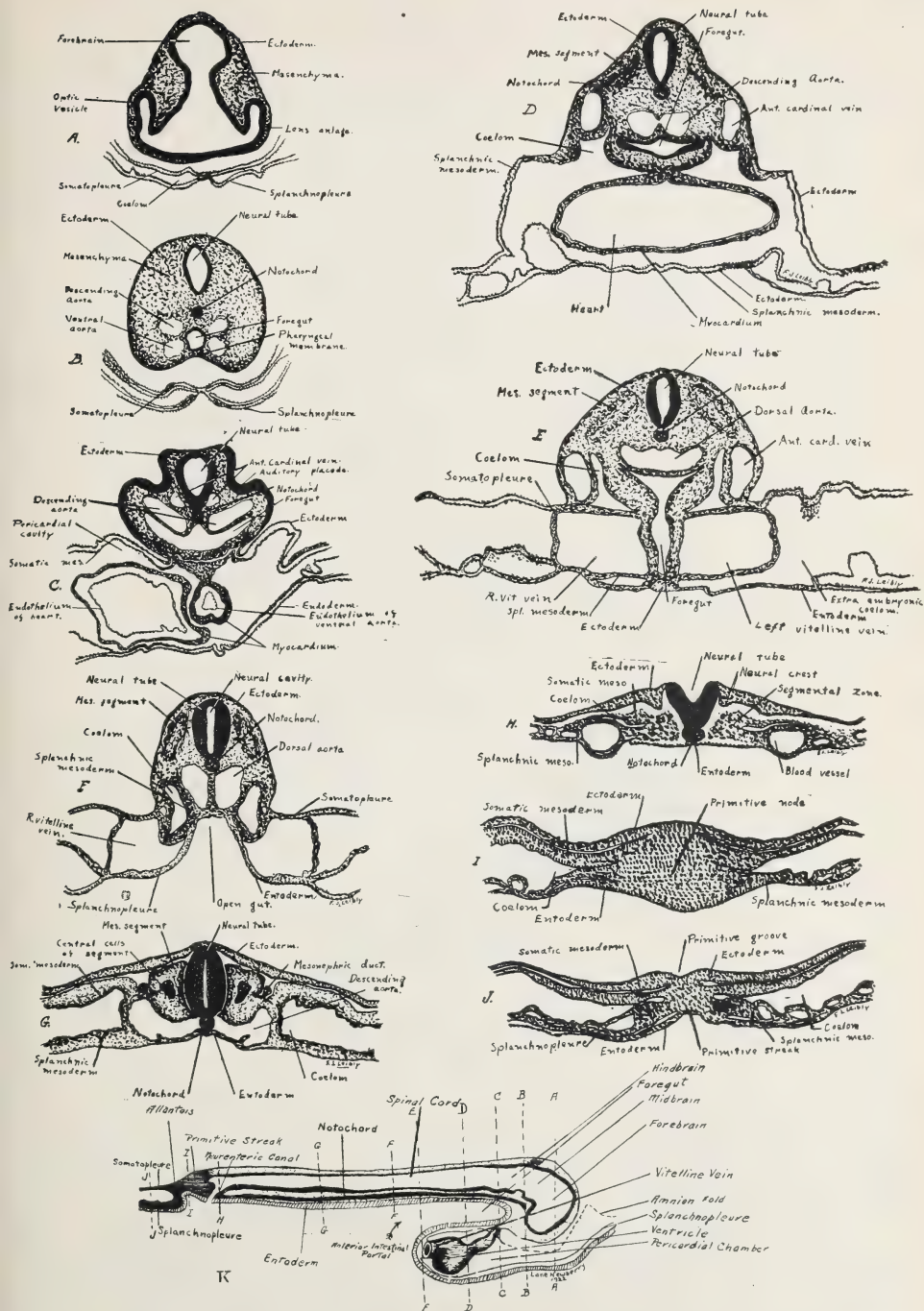


Fig. 280.

38 to 43 hour chick embryo (15 somites).

i, infundibulum; VIII, ganglion of eighth cranial nerve; A, atrium; V, ventricle.

**I**T IS at this period that the caudal end of the embryo becomes definitely outlined by the formation of a tail fold as well as lateral folds similar to the head fold.



Transverse sections through a 36 to 38 hour chick embryo. *A*, through forebrain; *B*, through the pharyngeal membrane; *C*, through hindbrain and auditory placodes; *D*, through posterior end of heart; *E*, through the intestinal portal; *F*, just posterior to *E*; *G*, through the fourteenth pair of segments; *H*, through the rhomboidal sinus; *I*, through Hensen's node; *J*, through the primitive streak; *K*, medial longitudinal section of a 36 to 38 hour chick embryo. (This drawing must be studied very carefully and thoroughly to understand the transverse sections which are cut through the levels marked.)

## THE BRAIN

Going on from where we left off in our discussion of the formation of the three primary brain vesicles, we find that at this period the neural canal has completely closed, even the rhomboidal sinus has fused. The primary vesicles have enlarged, and their lines of demarcation have become more definite. The fore-brain has grown forward as an unpaired vesicle from which the cerebral hemispheres are to develop. The walls of the brain itself lie under the ectoblast, while between the walls and the ectoblast can be seen a small amount of mesoblast which is to form the skull.

The optic vesicles have become elongated and definite constrictions

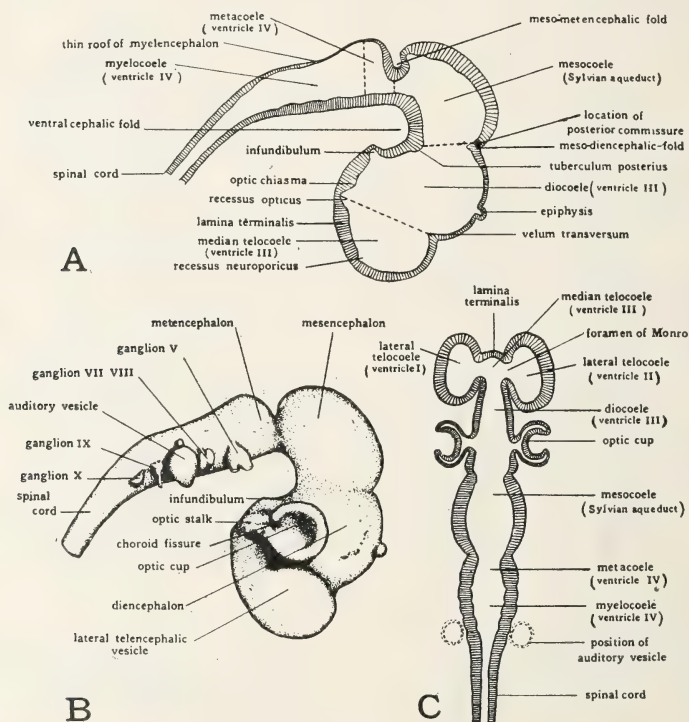


Fig. 282.

Diagrams of brain of 4-day chick embryo. Dotted lines show arbitrary boundaries between vesicles. *A*, longitudinal; *B*, right side; *C*, horizontal section. (From Patten, after V. Kupffer.)

are formed at their bases so that they now form **optic stalks**, which bend downward and backward.

The cranial nerves can also be seen developing at this period.

It is at this time that the first bend or **flexure** takes place in the brain, cephalad to the notochord (Fig. 282). This is the **cephalic flexure**.

If the neural plate be examined at the end of the first day, eleven enlargements (Fig. 278) will be seen with definite constrictions between

them. These enlargements are known as **neuromeres** and are really an uncompleted segmentation.

The literature of Embryology is filled with many varying and unsat-

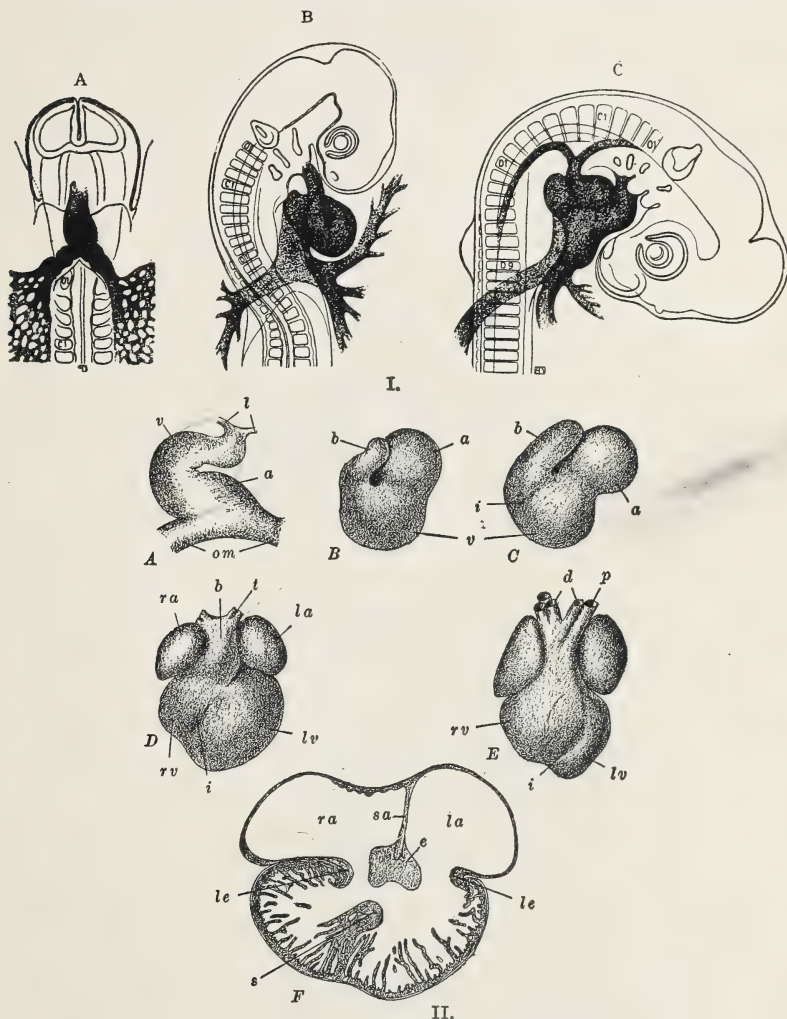


Fig. 283.

I. Views to show the posterior displacements of the heart in the chick embryo. *A*, The heart lies ventral to the first segment. This is the region where the future hindbrain will form. *B*, The point of bending loop of the ventricle is at the seventh cervical segment. *C*, The bending of the loop of the ventricle is now at the ninth thoracic segment. (From Corning after Duval.)

II. The development of the heart of the chick. *A-E*, ventral views of the heart; *A*, of a forty-hour embryo; *B*, of a 2.1 mm. embryo; *C*, of a 3.0 mm. embryo; *D*, of a 5.0 mm. embryo; *E*, of a 6.5 mm. embryo. *F*, Frontal section through the heart of a 9 mm. embryo. *a*, Auricle; *b*, bulbus; *d*, roots of dorsal aorta; *e*, median endothelial cushion; *i*, interventricular groove; *la*, left auricle; *le*, lateral endothelial cushion; *lv*, left ventricle; *om*, vitelline artery; *p*, left pulmonary artery; *ra*, right auricle; *rv*, right ventricle; *s*, interventricular septum; *sa*, interauricular septum; *t*, roots of aortic arches; *v*, ventricle. (*A*, *F*, after Hochstetter; *B* to *E* after Greil.)

isfactory theories as to what becomes of each neuromere, but as yet nothing can be demonstrated satisfactorily. It is conceivable, however, that as in the crayfish, for example, where we assume that each separate appendage or pair of appendages bespeak an embryological segment, so in vertebrates, where optic vesicles grow from the fore-brain, we may assume a fusion of several segments.

At about thirty-three hours, the floor of the prosencephalon has a depression formed in it, which is to become the *infundibulum*. This is an important seat of future development. It must, therefore, be studied carefully so that it can be recognized in future work.

At about thirty-eight hours, the three primary vesicles divide to form five vesicles (Fig. 278, 282).

The prosencephalon divides into **telencephalon** (end-brain), and **diencephalon** ('twixt-brain); the mesencephalon remains undivided; while the **rhombencephalon** divides into **metencephalon** (cerebellum and pons), and the **myelencephalon** (medulla oblongata).

The telencephalon has not yet completely separated from the diencephalon, but there is a median enlargement, showing where the division will take place.

The two most anterior neuromeres of the original rhombencephalon form the metencephalon, and the posterior four neuromeres form the myelencephalon.

At thirty-five hours, the auditory pits begin growing as thickened ectoderm, known as **auditory placodes**, on the dorso-lateral surface opposite the most posterior inter-neuromeric constriction of the myelencephalon. At thirty-eight hours, the general level of the ectoderm has become depressed to form a pair of cavities known as **auditory pits**. The pits seem to recede until they become closed vesicles, and separate from the superficial ectoderm, although it will not be until later that they form a definite connection with the central nervous system.

## TORSION

At about the time the cephalic flexure begins, there is also the beginning of a twisting of the entire embryo (Fig. 280), although at this time the twisting is only observable in the head region. The bending of the cephalic region downward is, as already stated, called "**flexion**." The twisting of the embryo from its ventral aspect to its side is known as "**torsion**."

As the yolk lies directly beneath the embryo, it can easily be understood that any bending ventrad would be stopped by the large mass of inert yolk beneath, so that, if there is to be any considerable bending at all, the entire embryo must turn on its side. This it does in all eggs which possess considerable yolk, though it does not necessarily come to lie on the same side in all amniotes. The chick turns so that **its left side lies next to the yolk**.

Torsion begins in the head region and gradually and slowly extends

the full length of the body, so that a whole mount, after torsion is completed, shows the embryo lying on its left side with head and tail close together, the entire embryo forming from one-half to about three-fourths of a circle.

### THE CIRCULATORY SYSTEM

By the end of the second day, the heart has become still more twisted, and is now S-shaped with the venous end above and behind the arterial end, so that both ends lie close together with the loop as an

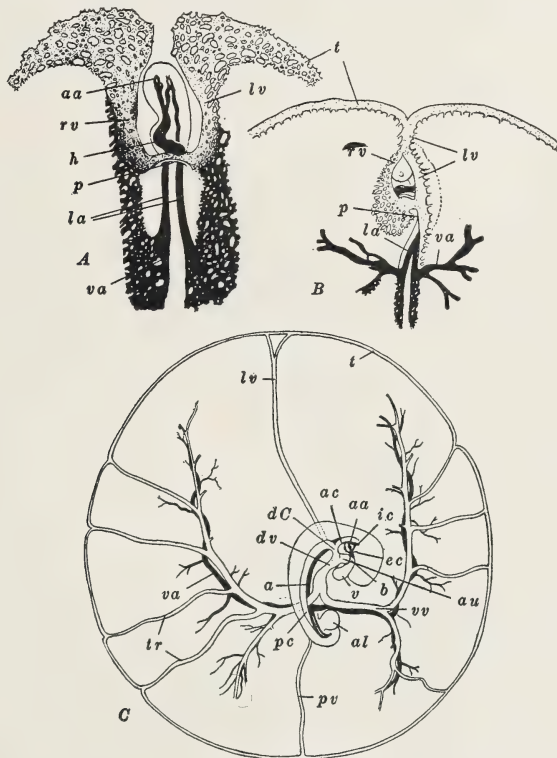


Fig. 284.

Diagrams of the circulation in the chick embryo and area vasculosa. The vascular network of the area vasculosa is omitted for the most part. *A*. Anterior and central parts of the embryo and vascular area at about thirty-eight hours ( sixteen pairs of somites). Viewed from beneath. *B*. Median and anterior parts of vascular area and embryo at about seventy-two hours (twenty-seven pairs of somites). Viewed from beneath. *C*. The main vascular trunks of the fourth day. *a*, Dorsal aorta; *aa*, aortic arches (first and second in *A*, second, third and fourth in *C*); *ac*, anterior cardinal vein; *al*, allantois; *au*, auricle; *b*, bulbus arteriosus; *dC*, ductus Cuvieri; *dv*, ductus venosus; *ec*, external carotid artery; *h*, heart; *ic*, internal carotid artery; *la*, lateral dorsal aorta; *lv*, left anterior vitelline vein; *p*, anterior intestinal portal; *pc*, posterior cardinal vein; *pv*, posterior vitelline vein; *rv*, right anterior vitelline vein; *s*, sinus venosus; *t*, sinus terminalis; *tr*, venous trunks of the area vasculosa; *v*, ventricle; *va*, vitelline artery; *vv*, vitelline or omphalomesenteric vein. (From Kellicott after Popoff and Lillie.)

intermediate portion between. The venous portion forms a swelling which later becomes the **auricles**, while the arterial end also enlarges to form the **bulbus arteriosus**. The point of the loop becomes the **ventricles** (Fig. 283).

It is toward the end of the second day that the pair of aortic arches which have bent dorsad (and continue separately as the paired dorsal aortae) unite behind the head to form a single vessel which comes to lie directly beneath the notochord. However, after running but a short distance caudad, the single aorta again divides into two vessels from which the large vitelline artery, already mentioned, is given off on each side. The dorsal aortae, now greatly diminished in diameter, continue into the tail.

The first pair of aortic arches formed are called the **mandibular aortic arches** (Fig. 284).

A second pair now form behind the first, and before the close of the day there may be still a third pair, all of which connect in a similar manner to the first, with the bulbus arteriosus and the dorsal aorta.

The sinus terminalis is now also much better developed than before, and a true circulation has been established, which can carry the yolk-food-granules (after these have been converted into usable food) to the embryo.

It is essential that a somewhat detailed knowledge of the circulation be obtained.

The blood is brought to the heart by the vitelline veins (Figs. 277, 284). The heart then contracts and forces it through the aortic arches into the dorsal aorta. Here it passes tailward, a small portion going into the tail itself; but the greater part is carried to the vascular area. There are two ways in which the blood now gets back into the vitelline veins. First, it may pass directly to the veins from the arteries through the connecting capillaries; or, second, it may pass into the sinus terminalis at a middle point on each side, and then pass forward and backward through this large vessel. The greater portion, however, in this second method passes forward toward the head from where it is returned to the heart through two large parallel vessels. The part which passes backward is again distributed to the vascular area, as there are no connecting vessels with the tail of the embryo. The vitelline veins and arteries run parallel to each other, though **the veins lie a little forward from the arteries**.

In the embryo itself, the **cardinal veins** are the main afferent vessels. At thirty-eight hours the **anterior cardinals** can be seen. These are a pair of vessels which return the blood from the head of the embryo to the heart. The **posterior cardinals** are also paired, and return blood from the caudal region.

Both anterior and posterior cardinal veins unite on each side of the body to form a short common vessel before entering the heart, the

right and left **ducts of Cuvier**, or **common cardinal veins**. These Cuvierian ducts then turn ventrad on each side of the fore-gut and enter the sinus venosus at the same point the omphalomesenteric veins enter.

The omphalomesenteric veins [so called because they pass through the umbilicus (navel) as umbilical vessels connecting the offspring with the mother in the higher forms], are established in the chick from thirty-three to thirty-six hours' incubation. They are postero-lateral extensions of the self-same endocardial tubes which formed the heart. They extend laterad to meet the vessels which develop in the vitelline plexus outside the embryo, and which extend inward toward the embryo. The **omphalomesenteric veins** (those lying within the embryo) eventually become one with the **vitelline veins** (those lying in the extra-embryonic area) and thus establish the **afferent vessels of the vitelline circulation**.

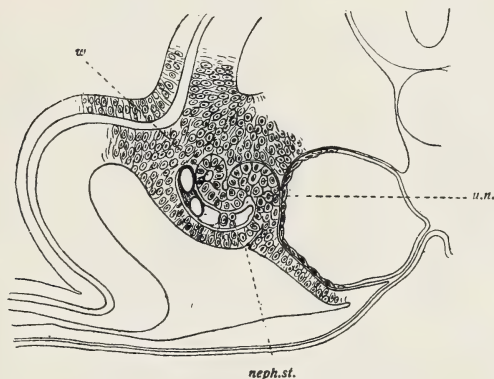


Fig. 285.

A portion of a cross section of a 54 hour chick embryo through the solid anlage of the pronephric tubules in the region of the beginning of the Wolffian duct. The nephrostomes are just beginning to form. *neph.st.*, nephrostome; *u.n.*, pronephric ducts; *w*, Wolffian duct. (After K  lliker.)

The **efferent** vessels develop at about forty hours. They have a dual origin. The embryonic vessels consist of the branches of the dorsal aortae which extend outward, where they meet with the extra-embryonic arteries growing toward the embryo to meet with, and become confluent with, the embryonic efferent vessels, now being known as the **omphalomesenteric arteries**.

It is at about the thirty-second hour that the heart begins to contract irregularly, although the maximum rate (150 to 180 per minute), is not reached until after one hundred hours of incubation.

### THE PATH OF A BLOOD-CORPUSCLE

It is well to follow a corpuscle through its entire circulation at this time. With the contraction of the heart, the corpuscle will be sent

through the ventral aortae, along the dorsal aortae, out through the omphalomesenteric arteries to the plexus of vessels on the yolk.

It will be remembered that various membranes surround the yolk. These contain many small vessels which absorb the yolk. As there must be an oxygenation of the blood, this vitelline circulation must also assist in this function until the allantois, shortly to be described, is formed. This aeration can be accomplished on account of the great area these membranes cover, which permits a wide field from which to draw the oxygen that permeates through the egg shell and the albumen surrounding the yolk.

After the yolk has been absorbed as food-material, and the blood has become oxygenated, the blood is collected into the sinus terminalis and the vitelline veins. The latter converge toward the embryo from all parts of the vascular layer, and empty into the omphalomesenteric veins, which return the blood to the heart.

The blood which has been sent to the various parts of the embryo has in the meantime been returned from the head region by the anterior cardinals, and from the caudal end by the posterior cardinals, the anterior and posterior cardinal of each side having met to form a short **common cardinal (duct of Cuvier)** through which the blood flows into the sinus portion of the heart.

There is, therefore, a **mixed circulation** in the heart, consisting of both embryonic and extra-embryonic blood. The extra-embryonic, of course, is the richer in both food and oxygen supply.

## THE EXCRETORY SYSTEM

After about ten somites have been formed, the beginnings of the excretory system are visible.

It will be remembered that the mid-region of the partially segmented mesoderm, known as the mesomere, is to become the excretory system. It can be noted first as a solid cord of cells, extending for two or three somites (Fig. 285). This will be called the **Wolffian Duct** as soon as a lumen forms.

During the second half of the second day, this solid rod elongates both headward and tailward, the more tailward portion becoming free and lying between ectoblast and mesoblast. A lumen appears toward its center and extends headward and tailward simultaneously. About the beginning of the fourth day the duct definitely opens into the cloaca.

The **Wolffian body** also makes its appearance on the second day, but it will be better understood if the description is reserved until later.

## CHAPTER VI

### EXTRA-EMBRYONIC MEMBRANES

IT WILL be remembered that, when the mesoderm splits into a somatic and a splanchnic layer, it extends out over the yolk so that there is no definite line of demarcation separating embryo from the surrounding media. First, the head fold appears, delimiting the embryo at the cephalic end, and later the tail-fold and lateral fold do the same for

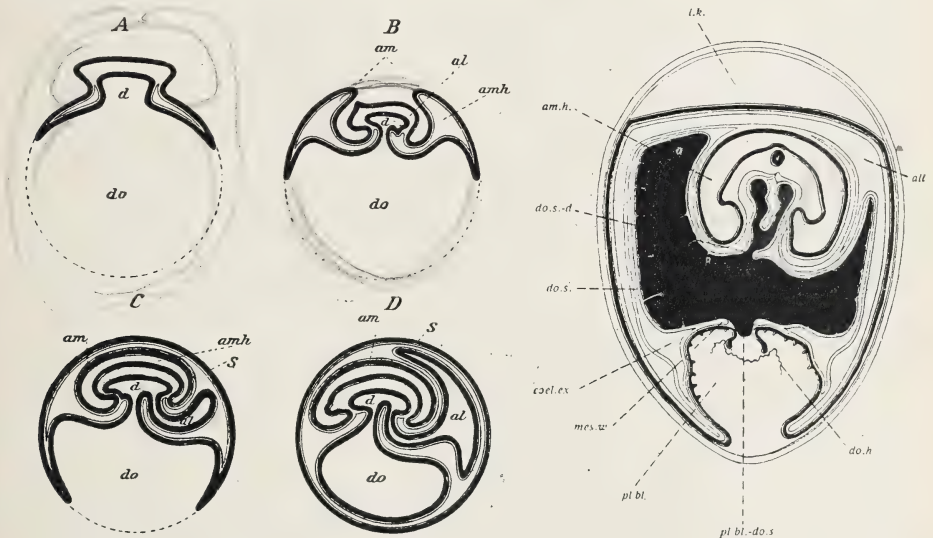


Fig. 286.

A, B, C, D, four stages of development of the embryonic membranes in birds. *al*, allantois; *am*, amnion, (in Fig. B., this forms folds which give rise to both amnion and serosa); *am.h.*, amniotic cavity; *d*, digestive cavity; *do*, yolk-sac.

E. Cross section through entire egg (including shell). *al*, allantois which begins developing at the blunt end of egg; *am.h.*, amniotic cavity; *coel.ex.*, extra-embryonic coelom; *do.s.*, yolk-sac showing development of mid-gut—*do.s.d.*; *do.h.*, covering of yolk; *l.k.*, air-chamber; *mes.w.*, extensions of the mesoderm between the communicating opening of yolk sac and amniotic cavity—*pl.bl.* The remaining portion of the yolk covering (*do.h.*) closes the passage. These mesodermal extensions as well as the lower tips, at the pointed end of the egg, close later and thus form a closed amniotic cavity. *pl.bl.*, amniotic cavity which develops from the ectoderm with tiny projections on the inner side. It is in this cavity that the remaining yolk is found; *pl.bl.do.s.* Communicating passage between amniotic cavity and yolk-sac. (A, B, C, D, after Boas, E, after Duval.)

the caudal and lateral regions. After these folds have bent downward and under the embryo, and almost separated the embryo from the yolk, we speak of the space between the somatic and splanchnic layers as the **intra-embryonic coelom** and the **extra-embryonic coelom**, according to which portion lies within, and which portion lies outside, the embryo.

The limiting folds, which are continuous with the head fold and

extend on each side of the embryo as the **lateral folds**, form the line of demarcation known as the **lateral limiting sulci**.

In this chapter we are concerned with the extra-embryonic membranes which are developed from the various layers in the extra-embryonic region. The membranes themselves are four in number: the **yolk-sac**, the **amnion**, the **serosa**, and the **allantois** (Fig. 270).

### THE YOLK-SAC

This is the first of the extra-embryonic membranes to appear. It must be remembered that, as the splanchnopleure grows outward from the embryo, it surrounds the yolk, thus forming the yolk-sac. The yolk itself forms the floor of the primitive gut.

As the underfolding in the head-region separates the head from the remaining blastoderm, it grows caudally and forms an entodermal floor to the primitive gut, and the part which thus obtains this entodermal floor is called the **fore-gut**. So, too, in the tail region a little later (about the third day), the tail folds under the posterior end of the embryo and the part which thus obtains an entodermal floor in that region is called the **hind-gut**. The portion between fore-gut and hind-gut is the **mid-gut**, which is, of course, that region where the yolk is still the floor. As the fore-gut and hind-gut become larger and extend toward each other, the mid-gut occupies less and less area, until there is merely a little duct something like the small end of a funnel, the larger end of the funnel being the extended splanchnopleure surrounding the yolk. In other words, the mid-gut consists only of the **opening of the yolk-stalk**, which latter is made up in turn of the walls of the splanchnopleure drawn together at this point.

As the neck of the yolk-sac is thus constricted, the omphalomesenteric arteries and veins, which extend throughout the region where the constriction takes place, have likewise been drawn into the constricted area, and pass to and from the embryo through the yolk-stalk, side by side.

The yolk is now covered with a vascular network spreading throughout the splanchnopleure of the yolk-sac, so that the entire food supply of the embryo comes to lie in a sac with this circulation of its own definitely attached to the mid-body region, though as far as we know, no yolk granules pass directly into the embryo, all of it being absorbed by the vascular network. In older embryos, the yolk-sac even folds considerably, so that a still greater expanse of vascular area is established.

The white albuminous portion of the egg rapidly loses the water it contains, and is absorbed by the extra-embryonic membranes.

Ultimately (about the nineteenth day) the yolk-sac is completely enclosed within the embryo and then rapidly disappears until it is entirely gone by the sixth day after hatching.

## THE AMNION AND THE SEROSA

While the splanchnopleure forms the yolk-sac, it is the somatopleure, lying outside the embryo, from which both amnion and serosa are derived.

At about thirty hours, the first observable portions of the amnion appear as a crescentic fold with the concavity toward the head of the embryo. This fold must not be confused with the head fold of the chick which folds under the embryo.

The head at this time sinks into the yolk to a slight degree, just as the extra-embryonic somatopleure anterior to the head is thrown into the head-fold of the amnion. As the embryo grows anteriorly and the somatopleure caudally, the amniotic fold which is thus folded upon itself, forms a double-walled cap over the head of the embryo, gradually extending more and more caudad. The caudally directed limbs of the head-fold of the amnion continue growing posteriorly on each side of the embryo, where they are known as lateral amniotic folds. These grow dorsad and mesiad, finally meeting in the midline.

During the third day, the amniotic tail-fold develops and grows cephalad to meet the structures just mentioned, thus forming a complete envelop for the embryo. The place where the various amniotic folds meet is called the **amniotic raphe**.

The amnion is now a completed saccular structure filled with a fluid in which the embryo is free to move about and change its position. In all probability this ability of free movement also prevents adhesions and consequent malformations.

It is to be noted that the manner in which the amniotic folds came into existence, has caused the innermost portions to be ectodermal. This ectodermal layer is continuous with the ectoderm of the embryo.

Likewise, the manner of the somatopleure folding upon itself, as it does, causes **two walls to cover the embryo**. The inner one is the ectodermal layer just mentioned, and the outer one is known as the **serosa**. There is a **sero-amniotic cavity** between the two.

The somatopleure now extends peripherally until the entire yolk-sac, as well as the embryo, is covered with serosa.

The allantois extends between serosa and amnion.

## THE ALLANTOIS

This structure differs from the amnion and yolk-sac in that it develops **within the embryo proper**, though it does extend out into the extra-embryonic region as it develops.

About the third day, the allantois develops by an outpushing of the ventral wall of the hind-gut (entoderm), pushing the splanchnopleure ahead of it, so that we may say it is composed of splanchnopleure with an entodermal lining. The following day it pushes out of the embryo

into the extra-embryonic coelom, the attached end lying caudal to, and parallel to, the yolk-stalk. The proximal portion is the **allantoic stalk**, while the extended bladder-like distal portion is the **allantoic vesicle**.

It grows very rapidly from the fourth to the tenth day, and extends into the sero-amniotic cavity in a flattened manner. Ultimately it encompasses the entire embryo and yolk-sac, and in so doing the mesodermic layer of the allantois fuses with the layer of mesoderm of the serosa which comes to lie in direct contact with it. This means that there is thus formed a double layer of mesoderm, the serosal portion derived from the somatic mesoderm, and the allantoic portion derived from the splanchnic mesoderm. A very rich vascular network now develops between these two layers, connected with the vascular circulation by the allantoic arteries and veins.

The allantois thus becomes an organ of respiration, as well as of circulation, to the developing embryo. As the allantois lies just beneath the porous shell, a wide area is presented for an exchange of the carbon dioxide developed within the embryo and the oxygen from the outer world.

In addition to this function, however, the allantois also serves as a reservoir for the secretions from the excretory organs of the embryo, and likewise takes part in absorbing the albumen.

### THE CHORION

The serosa will become a part of the **chorion** in the higher forms, and consequently, should be clearly understood at this point. The allantoic vessels mentioned above and the mesoderm which lies between the serosa and amnion, later fuse with the inner layer of the serosa to form the **chorion**, which is the embryo's organ of attachment to the uterine wall of the mother. How very important the allantoic circulation becomes in mammals may be surmised by realizing that there is little yolk in mammalian eggs, which, consequently, forces the embryo to receive all of its nourishment from the blood of the mother through the uterine walls. The allantoic circulation thus performs the function of the vitelline circulation also.

## CHAPTER VII

### DEVELOPMENT OF THE THIRD DAY

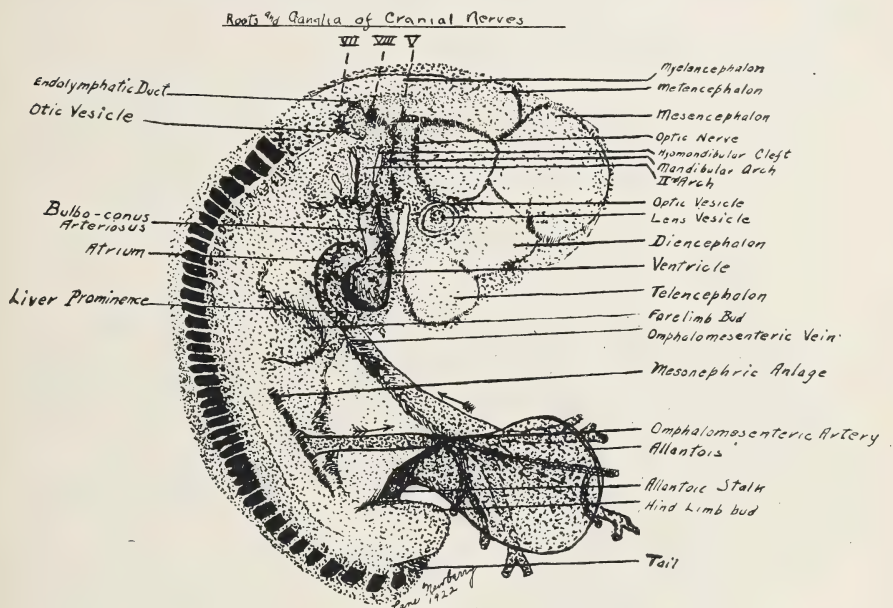


Fig. 287.

64-hour chick embryo. (41 somites.)

IT IS on the third day that more structures make their first appearance than on any other single day of the chick's entire embryonic life. The blastoderm itself has increased in size so that it covers almost one-half the yolk surface. The white of the egg has decreased in amount so that the vascular area has been brought closer to the surface under the shell, making aeration of the blood easier.

The sinus terminalis reaches its greatest functional activity during this day, and the vitelline veins have been brought in close contact with the vitelline arteries by the growth of the embryo.

The blood, which the vitelline, or omphalomesenteric, arteries bring to the sinus terminalis, still flows headward and tailward as before. The portion flowing toward the head returns to the embryo through two large vessels lying parallel to the long axis of the embryo, but sometimes there is only one of these—the one emptying into the left vitelline vein. Even if the two vessels are present, the left is the larger.

It is on the third day also that the single posterior vessel, which

also empties into the left vitelline vein and carries blood from the posterior region of the sinus terminalis, makes its appearance.

It will be remembered that it is during this day that the torsion of the embryo takes place from the head region posteriorly, so that **cross sections made from the anterior end will show the embryo turned upon its left side, while in the posterior region it still lies upon its ventral surface.**

The flexion continues also, so that the mid-brain becomes the most anterior region of the embryo. This flexion not only brings the fore-brain in close relation to the heart, but brings optic and otic vesicles opposite each other. It will be remembered that the eye-pits form in the fore-brain and the auditory pits in the medulla oblongata.

### THE NERVOUS SYSTEM

All parts are growing, and have become larger than on the second day (Fig. 288). The important new developments are as follows:

**The epiphysis** appears as a small evagination in the midline on the dorsal surface of the diencephalon. It later becomes the **pineal gland**.

**Rathke's Pocket** (Fig. 301, 1) is an ectodermal invagination which has folded in just beneath the infundibulum. This pocket soon loses its connection with the outer epithelium and then becomes permanently associated with the infundibulum to form the **hypophysis** or **pituitary body**.

### THE OPTIC VESICLES (Fig. 289)

It will be remembered that these were originally broad stalks directly continuous with the cavity of the fore-brain. The cavity, or lumen, of the optic stalks is then called an **optocoele**, and the cavity, or lumen, of the prosencephalon is called the **prosocoele**. A constriction formed earlier is very marked at about fifty-five hours. The distal ends have invaginated, forming a double-layered cup. The newly indented layer is termed the **sensory layer**, because it is from this that the sensory layer of the retina is to be formed. The underlying layer is called the **pigment layer**, because it is from this that the pigmented layer of the retina is to arise. The invaginated cups are often called **secondary optic vesicles** to distinguish them from the original vesicles before invagination. The original vesicles are then known as **primitive vesicles**.

The optic cup does not invaginate so as to form an equally rounded edge. The invagination begins at the ventral surface and continues dorsally and toward the midline, so that at the place where the invagination began, there is a region which has no definite lip. The cup, therefore, looks more like a cup that has had this portion broken out. This lipless region is known as the **choroid fissure**.

The invagination continues for the length of the optic stalk, thus

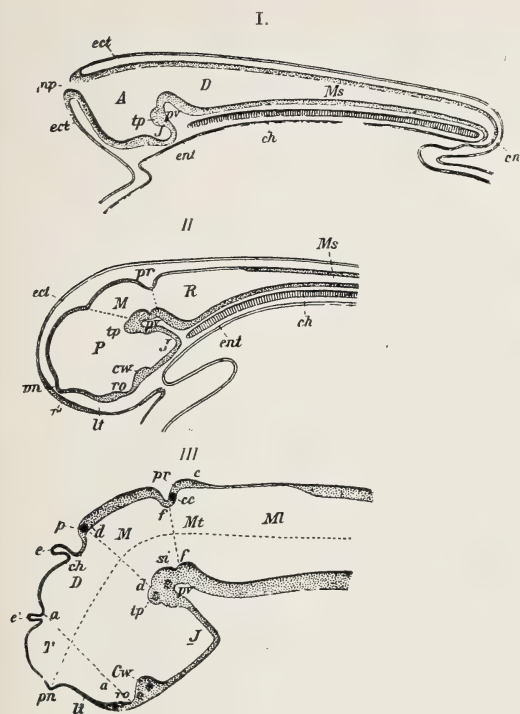


Fig. 288.

Diagrams showing brain development in vertebrates. Longitudinal sections.

I. Before the blastopore closes.

II. At the time three regions can be seen.

III. At the time five brain regions have formed. (Compare with Fig. 281.)

A, prosencephalon; aa, dividing line between telencephalon and diencephalon; c, cerebellum; cc, cerebellar commissure; ch, (in I and II) dorsal nerve cord; (in III) habenular commissure; en, neurenteric canal; cp, posterior commissure; cw, thickening on optic nerve due to the crossing of fibers (this is the chiasma); D, diencephalon; dd, line separating diencephalon and mesencephalon; e, epiphysis; e', paraphysis; ect, ectoderm; ent, entoderm; ff, line dividing mesencephalon and metencephalon; J, infundibulum; lt, lamina terminalis; M, mesencephalon; Ml, myelencephalon; Ms, spinal chord; Mt, metencephalon; np, neuropore; P, prosencephalon; p, pr, pn, neuroporic process; pv, ventral brain-fold; R, rhombencephalon; r, thickening of ectoderm which is sometimes said to be the anlage of an unpaired olfactory groove; ro, optic recess; si, the groove (sulcus intra-encephalicus) which forms the hindermost boundary of the midbrain; T, telencephalon; tp, tuberculum posterius (After von Kupffer.)

forming a fissure in the stalk along which, and in which the optic nerves and blood-vessels come to lie. This is on the ventral surface of the stalk. In the meantime, the optocoele has practically become obliterated, a very small portion alone remaining between the sensory and pigment layers in the optic cup. Even these fuse shortly, and then the optocoele entirely disappears.

The eye lens arises independently of the optic vesicles in the ectoderm, close to the vesicle. At forty hours the ectoderm in this region has thickened. The placodes thus formed grow toward and into the optic cups after themselves forming vesicles. The superficial ectoderm from which they arise, soon closes again at the point where the lenses have arisen, although a very small opening may still be seen for a short time.

It is well to call particular attention at this point to the similarity of the way in which the lens of the eye and the auditory vesicle develop by a thickening of ectoderm, then insinking and finally completely separating from the superficial ectoderm from which it sprang. The lesson to be brought home, is that, once these structures have separated from the superficial ectoderm, regardless of their original similarity, each follows a totally different line of development and differentiation so as to become structurally and functionally unlike in the adult condition. **This original similarity and adult divergence** should be noted throughout embryological and comparative studies.

In the myelencephalic portion of the brain, the neuromeres have lost their dorsal constrictions, though they can still be seen on the lateral and ventral surfaces, while the whole cord has thickened. This thickening constricts the lumen so that it is quite slit-like at this time. The neural tube has closed completely at both anterior and posterior ends at this period.

It will be remembered that the neural, or medullary, plates have formed, and their lateral folds have begun to unite to form the neural groove. This union has now been completed. The ectoderm, dorsal to

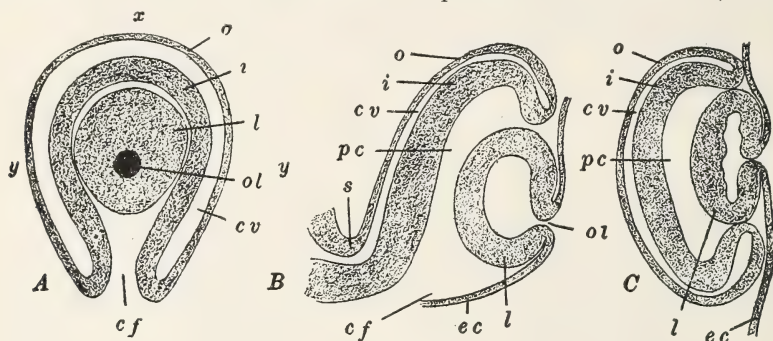


Fig. 289.

Diagrams of sections through the eye of the chick embryo at the end of the second day. The dorsal margin is toward the top of the page in *A* and *B*. *A*. Eye as viewed directly. *B*. Vertical section through the line *x-y*, in *A*. *Cf*. Choroid fissure; *cv*, cavity of primary optic vesicle; *ec*, superficial ectoderm of head; *i*, inner or retinal layer of optic cup; *l*, lens; *o*, outer or pigmented layer of optic cup; *ol*, opening of lens sac from surface of head; *pc*, posterior chamber of eye; *s*, optic stalk, continuous with the floor and lateral wall of the diencephalon. (From Lillie "Development of the Chick," by permission of Henry Holt & Co., Publishers.)

the groove, has again become continuous, leaving a slight area between neural groove and superficial ectoderm.

It will also be remembered that there are small groups of cells on each side of the midline, lying within this area, which we called **neural crests**, to distinguish them from the neural folds with which they were in close connection.

The two crests lying on each side of the midline fuse for a time, but because they began as two separate groups, they again become separate in a short time. They also form a sort of column on each side of the midline, running along the long axis of the embryo, but soon they segment and become the **dorsal root ganglia**, or **sensory ganglia**, of the spinal nerves (Fig. 290). As the segmented portions of these neural crests also extend into the head region, they there give rise to the ganglia of the **sensory cranial nerves**.

## THE DIGESTIVE TRACT

At the period we are describing, the fore-gut has extended from the anterior intestinal portal as its posterior limit to the infundibulum as its anterior limit. It is divided into a **pharyngeal portion**, lying

ventral to the myelencephalon and encircled by aortic arches, and an **oesophageal portion**, lying posterior to the pharyngeal with a much smaller lumen than the pharynx.

At this time there is an outpushing of the ventral portion of the pharynx and an inpushing from the ectoderm close to this region, which will soon meet and form the mouth-opening. The ectodermal inpushing

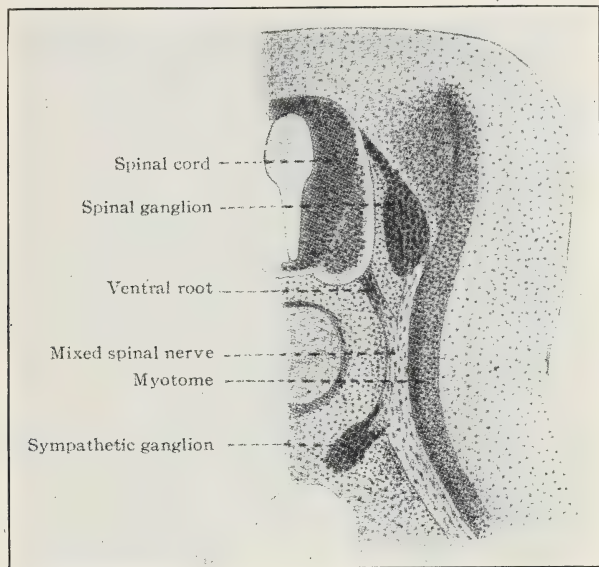


Fig. 290.

Developing nerve roots in a chick of 4½ days.  
(After Neumayer.)

is known as the **stomodaeum**, and the thin layer of tissue between the inpushing and outpushing, which is later to break through to complete the mouth-opening, is called the **oral plate**. (Fig. 301, I, Seessel's pocket.) It is this oral plate region in the adult which separates the oral cavity from the pharynx.

The fore-gut extends into the head region cephalad to the stomodaeum, and this portion is called the **pre-oral gut**. This pre-oral gut, however, disappears shortly after the oral plate breaks through, leaving only a small diverticulum which is then called **Seessel's pocket**.

The digestive tract has been lying close to the notochord up to this time, being separated from the notochord and the aortae by a broad thin layer of mesoderm. Now it begins to draw ventrad from this position, remaining attached, however, by the **mesentery**, a constantly narrowing band of tissue.

This mesentery is composed of mesoblast continuous with that which surrounds the entoderm of the digestive canal. The mesoblast consists of an undifferentiated middle layer (Fig. 291, b), in which blood

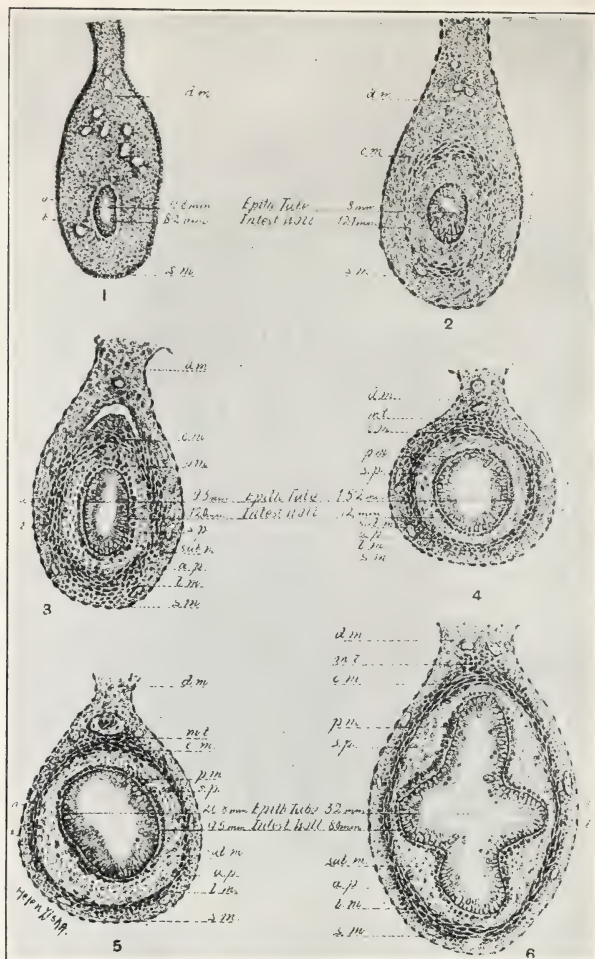


Fig. 291.

## Development of Digestive Tract.

- 1 Transverse section of descending colon 10-mm. pig.
- 2 Transverse section of descending colon 14-mm. pig.
- 3 Transverse section of descending colon 20-mm. pig.
- 4 Transverse section of descending colon 25-mm. pig.
- 5 Transverse section of descending colon 31-mm. pig.
- 6 Transverse section of descending colon 46-mm. pig.

## ABBREVIATIONS

- a.*, serosa.  
*b.*, undifferentiated middle layer.  
*dm.*, dorsal mesentery.  
*cm.*, inner circular smooth-muscle layer.  
*lm.*, outer longitudinal smooth-muscle layer.  
*mt.*, mesenteric taenia muscle band.  
*sp.*, Meissner's plexus (submucous).  
*ap.*, Auerbach's plexus (intermuscular).  
*sm.*, serosa.  
*subm.*, submucosa.  
*p.m.*, primordial mucosae cells.

N. B.—Note especially rapid increase in width of epithelial tube and the absolute decrease in thickness of mesenchymal wall due to tension stresses elicited by the growth of the former. (Eben J. Carey in The Anatomical Record, Vol. 19, No. 4.)

vessels are developed later, and a superficial layer (Fig. 291, a), of epithelium, continuous with the epithelial lining of the peritoneal cavity. The withdrawal of the anterior part of the fore-gut from the notochord is slight, as little or no mesentery is developed in that region.

It is interesting to note here that the oesophagus has its lumen closed for almost its entire length during the sixth day, only to reopen from the posterior region anteriorly again in about two days by the rapid growth of the epithelial tube. This latter grows in a circular direction on account of the outer pressure.

The portion of the intestinal tract immediately posterior to the oesophagus becomes dilated on this day to form the stomach. This is followed posteriorly by a short region recognized as the duodenum, because the beginnings of the liver and pancreas can be observed. Mesenchymal cells gather about the oesophagus and stomach from which their muscular and connective tissue coats will be derived.

There will be seen a small pitting-in of the ectoderm to meet the underlying entoderm, where the anal opening is to appear. However, this posterior opening does not open into the digestive tract until about the fifteenth day of incubation. The indenture, which is to become the anal opening, is called the **proctodaeum**.

The digestive tract is almost straight until the sixth day. Then the various loops form and the gizzard develops as a thick-walled outgrowth from the end of the stomach.

## THE LUNGS

Two small hollow outgrowths from the ventral side of the oesophagus near its anterior end are seen on the third day, the oesophagus itself becoming constricted at the point of outgrowth.

These constrictions form two divisions, the more dorsal becomes the oesophagus; and the ventral portion, the **trachea**. At the point where oesophagus and tracheae are continuous, the **glottis** will be formed.

The trachea grows caudad and bifurcates to form pairs of **lung-buds**. These lung-buds extend outward into the surrounding mesenchyme lying on either side of the midline. The splanchnic mesoderm is pushed ahead of the growing lung-buds, until it covers them and forms their outer investment layer or pleural covering. The entoderm of the intestinal tract, from which the trachea evaginated, forms the entire lining of trachea, bronchi, and all air-chambers in the

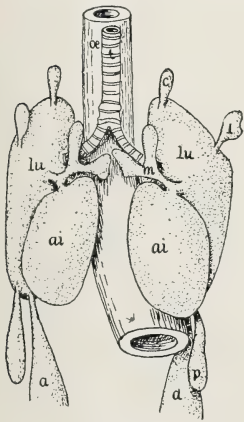


Fig. 292.

Ventral view of lungs and air-sacs of 12 day chick embryo. *ai*, anterior intermediate sac; *a*, abdominal sac; *c*, cervical sac; *l*, lateral part of interclavicular sac; *lu*, lung; *m*, mesial part of interclavicular sac; *oe*, oesophagus; *p*, posterior sac; *t*, trachea. (From Kingsley after Locy and Larsell.)

adult lungs. The connective tissue stroma of the lungs, however, is derived from the mesenchyme surrounding the lung-buds.

In the chick, as in all birds, there is a characteristic thin-walled, sac-like outgrowth from the hinder edges of the lungs to form the air-sacs (Fig. 292). These do not appear until about the eighth day.

### THE LIVER

The liver arises as a ventral diverticulum from the duodenum. It can be seen for a short time on the lip of the anterior intestinal portal, growing cephalad toward the fork where the omphalomesentric veins enter the sinus venosus. The liver grows out as a series of cords, pushing the splanchnic mesoderm ahead of it as its investing layer.

The liver evagination, as it forms, retains its opening into the duodenum (Fig. 293), which later differentiates somewhat to become the common bile duct, the hepatic and cystic ducts, as well as the gall bladder. Cellular cords bud off from the diverticulum and become the hepatic tubules which have secretory functions.

As the intestinal portal moves caudad when the fore-gut lengthens, the proximal portions of the omphalomesenteric veins come together and fuse in midline. The fusion extends caudad nearly to the level of the yolk-stalk, beyond which they still remain separate. The liver now surrounds the fused portion of the omphalomesenteric veins.

It will be noticed, therefore, that the yolk materials

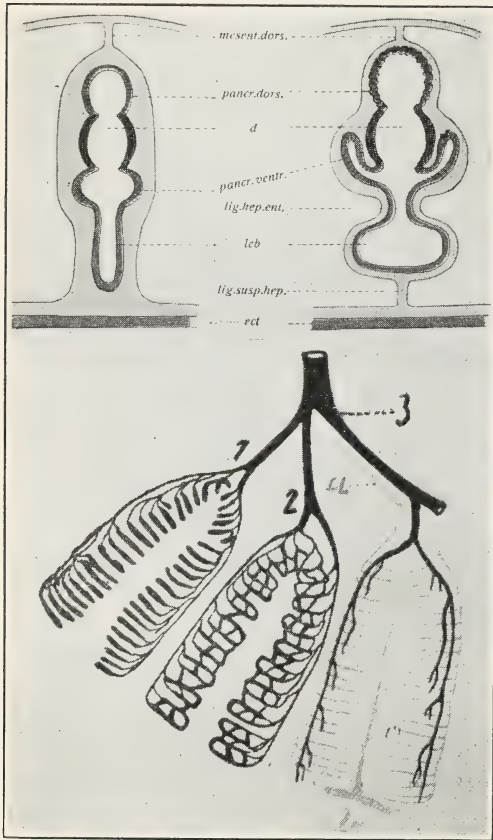


Fig. 293.

Two upper cuts are diagrams to show the development of the liver, pancreas, and hepatic ligaments. *d*, intestine; *ect*, ectoderm; *leb*, liver anlage; *lig. hep. ent.*, ligamentum hepato-entericum; *lig. susp. hep.*, ligamentum suspensorium of the liver; *mesent. dors.*, dorsal mesentery; *pancr. dors.* and *pancr. ventr.*, dorsal and ventral pancreas. (After Schimkewitsch.)

Lower cut is a diagram to show the development of the liver. Lobule 1 shows the principal parts of the gall capillaries; Lobule 2, shows the anastomoses of these gall capillaries; in Lobule 3, only the efferent bile capillaries are shown, together with the arterial and venous capillaries. *a*, arteries; *b*, veins. (After Stohr.)

must already at this early period pass directly into and through the liver. If this is remembered, it will make the adult portal circulation the better understood.

## THE PANCREAS

The pancreas arises as three diverticula from the duodenum at the approximate level of the liver diverticulum. There are three pancreatic buds: one medial bud, lying dorsal to the duodenum, and a pair of ventro-lateral buds.

The median bud appears at about seventy-two hours, while the two ventro-lateral buds can be seen at the end of the fourth day. The dorsal bud arises directly opposite the liver, and grows into the dorsal mesentery; while the ventro-lateral buds arise at the point where the liver connects with the intestine, so that both the liver duct and the ventral pancreatic duct open into the duodenum by a common duct, called the **ductus choledochus**. Cellular cords grow into masses from the three buds, fusing into one glandular mass with two ducts remaining, although sometimes all three remain.

## THE THYROID GLAND (Fig. 294)

This arises as a median diverticulum from the floor of the pharynx at the level of the second pair of gill pouches. By the close of the fourth day, the solid rod-like diverticulum, lying in a longitudinal position under the floor of the pharynx, has become saccular and remains connected with the point of origin as the **thyro-glossal duct** opening at the root of the tongue. In mammals, there are additional evaginations at the lateral region of the fourth gill pouch. By the sixth day, the thyroid body in the chick becomes bi-lobed, the lobes sending out cords of tissue which become hollowed out to form the regular adult thyroid tissue.

The gland then shifts backward and becomes surrounded with a sheath of vascular connective tissue.

## THE THYMUS GLAND (Fig. 294)

This organ arises from the posterior faces of the third and fourth gill pouches after the fourth day of incubation. While the organ is originally epithelial in character, there is soon an ingrowth of mesenchyme and the thymus then becomes chiefly lymphoid in structure.

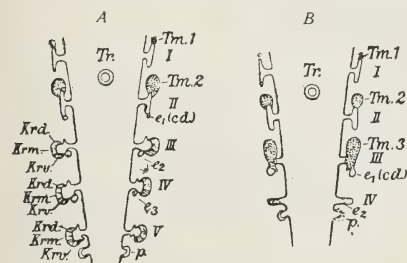


Fig. 294.

Diagrams to show the development of the derivatives of the digestive tract in the branchial region. A, *Anura*, B, *lizard*. *cd*, carotid gland; *e*<sup>1</sup>-*e*<sup>3</sup>, epithelial bodies; *Krd*, dorsal, mid, and ventral remains of the axial portions of the gill pouches; *p*, postbranchial bodies; *Tm*<sup>1-3</sup>, Thymus anlage; *Tr*, Thyroid gland; I-V, Gill slits. (After Maurer.)

## THE VISCERAL CLEFTS AND VISCERAL ARCHES

Different parts of the embryo grow at different rates of speed, and while the heart was formed directly under the anterior end of the digestive tract on the second day, on the third day the heart has shifted its position so far posteriorly that there is a distinct space between it and the head proper. This space we may call the neck or **pharynx**.

It is in this region that the mesoderm has not divided into the two layers—the somatic and splanchnic. We, therefore, still have a sort of sheet, consisting of the three primitive layers of ectoderm, mesoderm, and entoderm, extending outward from the embryo.

The entodermal lining of this neck region becomes pushed out into four narrow pockets (Fig. 295, A), called the **visceral**, or **gill**, **pouches**, during the latter part of the second or the early part of the third day. These meet with ectodermal depressions formed as furrows which grow inward to meet the gill pouches. The thin wall between the outpushings and the ectodermal inpushings breaks through in the lower forms, such as in fish and amphibia, and there remains open throughout life; but in the chick the opening is seen in the first three pairs during the first three or four days. It remains open for about two days. These openings, or places where openings usually occur, are known variously as **visceral clefts**, **gill clefts**, or **branchial clefts**.

As the neck is considerably curved, these clefts do not lie parallel to each other, but converge toward the ventral part of the neck. The fourth cleft never opens in the chick.

Numbering and naming these clefts begins with the most anterior and continues caudad.

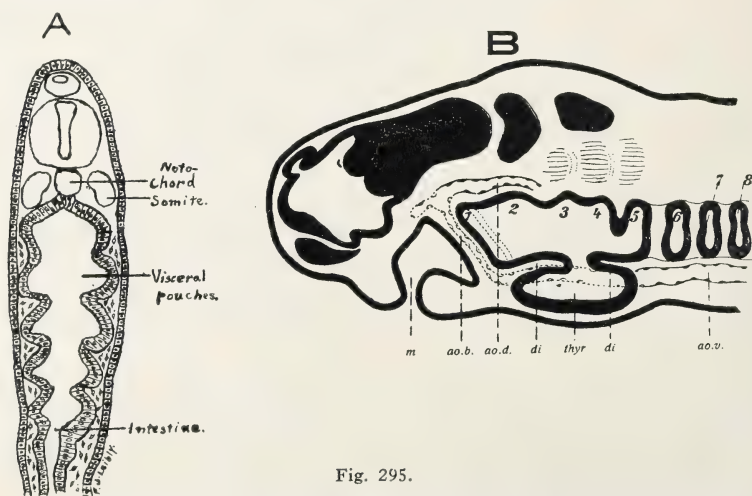


Fig. 295.

A, Horizontal, and B, longitudinal section through the head region of *Ammonoetes* (larval stage of lamprey). *ao.b.*, anterior aortic arch; *ao.d.*, dorsal aorta; *ao.v.*, ventral aorta; *di*, invagination which separates the anlage of the thyroid gland from the digestive tract; *m*, anlage of mouth; *thy.*, thyroid anlage; 1, ciliated gill region which probably becomes the spiracle; 2-8, gill pouches. (A, after Vialleton; B, after Dohrn.)

The first cleft is called the **hyomandibular cleft**, while the remaining ones are known respectively as the II, III, and IV, **gill clefts**.

Between these clefts, as well as immediately anterior and posterior to them, there is a pair of thickened regions, each pair of which meets ventrally in the midline and merges with its mate from the opposite side of the body. These thicknesses are called **visceral arches**, **gill arches**, or **branchial arches**, also numbered from the anterior end, caudad. The first is called the **mandibular**, the second the **hyoid**, and from here caudad the III, IV, and V.

The hyomandibular cleft lies between the mandibular and hyoid folds or arches.

It is well at this point to anticipate a little what is to become of these structures later (Fig. 296).

All the clefts close with the exception of the hyomandibular. This, too, begins closing at the end farthest from the pharyngeal opening, but retains the opening into the pharynx. The unclosed end itself becomes the **tympanic cavity**, while the remaining portion of the cleft becomes the **Eustachian tube**.

The external auditory meatus is formed by a depression in the sur-

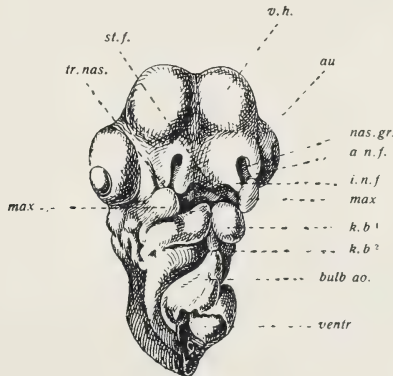


Fig. 296.

Head of a  $5\frac{1}{2}$  day chick-embryo. *a.n.f.*, lateral nasal process; *au.*, eye; *bulb.ao.*, bulbus aortae; *i.n.f.*, inner nasal process; *k.b.*<sup>1</sup> and *k.b.*<sup>2</sup> mandibular and hyoid arches; *max*, upper process of the mandibular arch; *nas.gr.*, nasal groove; *st.f.*, frontal process; *tr.nas.*, tear-duct running to nasal cavity; *ventr.*, ventricle; *v.h.*, forebrain. (After Duval.)

face ectoderm opposite the position of the tympanic cavity. The outer end of the closed hyomandibular cleft thus lies between the tympanic cavity and the external auditory meatus, the tissue formed by the closure of the cleft forming the tympanic membrane.

The most posterior two gill arches or folds entirely disappear in the adult stages of the chick.

The pair of mandibular arches grow toward each other on the ventral side and fuse to form the basis of the **mandible**, or lower jaw. From

the dorsal end of each mandibular arch and at their anterior edge, a small branch grows downward and forward during the fourth and fifth days, such branch, or branches, being called **maxillary processes**. There is a triangular median process growing toward these maxillary processes from the front of the head, known as the **fronto-nasal process**. The maxillary processes form the upper jaw or the maxillary bones. The maxillary processes do not fuse with each other, but to each side of the fronto-nasal process. When this union does not become complete, the well-known abnormality of **hare-lip** results.

The formation of clefts and arches may be understood the better by the following illustration from Professor Reese:

With the hands in front of the body (the palmar aspect of each hand directed mesiad), and pointed downward, "bring the tips of the fingers together, the fingers of each hand being slightly separated. The thumbs should, at first, be closely pressed against the forefingers, and should be considered as fused with them. If the fingers and hands are slightly bent, there will be a space between the two hands that may be taken to represent the pharynx of the chick, while the four fingers will represent the first four gill arches, and the spaces between the fingers will represent the first three gill clefts. The closure of the visceral clefts may be represented by bringing the fingers of each hand together. The forefingers, which should, in reality, be the only ones which actually meet in the midventral line, will represent the mandibular arch, forming the lower half of the mouth. The formation of the maxillary arch, by processes budded out from the upper ends of the mandibular arch, may be represented by separating the thumbs from the forefingers, and pointing them toward each other without letting them come in contact; the triangular space between the thumbs, thus held, being fulfilled in the imagination by the fronto-nasal process. The angles between the thumbs and forefingers will represent the angles of the mouth. Of course, to make the comparison more striking, there should be one more finger to represent the hindermost arch and cleft, but as the hinder arches and clefts form no part of the adult chick, this omission is of little importance."

### THE CIRCULATORY SYSTEM (Fig. 297)

As has been stated, there are already present two or three pairs of aortic arches by which blood is carried from the bulbus arteriosus around the pharynx to the dorsal aorta. It will be noted that the first aortic arch lies in the first (mandibular gill arch), the second in the hyoid fold, and so on, each bearing a distinct relation to the correspondingly numbered gill-fold.

The heart, which it will be remembered is attached only at the cephalic and caudal ends, is growing rapidly and twisting upon itself. The venous, or atrial, side is the more stationary. This side, originally,

lay caudal to the arterial, or conus, end of the heart, but in the twisting, the conus end comes to lie caudal to the sinus, or venous, end, a position that the higher vertebrates all retain in the adult stage. In fishes, the atrial region of the heart remains caudal to the ventricular portion even in the adults.

The point where the two vitelline veins meet to empty into the heart becomes pushed farther and farther caudad, so that the two veins unite to form a common opening into the heart. All blood from the vascular area to the heart passes through this single common tube, though in a short time the right vein will dwindle away and disappear. The tube is then an opening for the left vitelline vein only. This com-

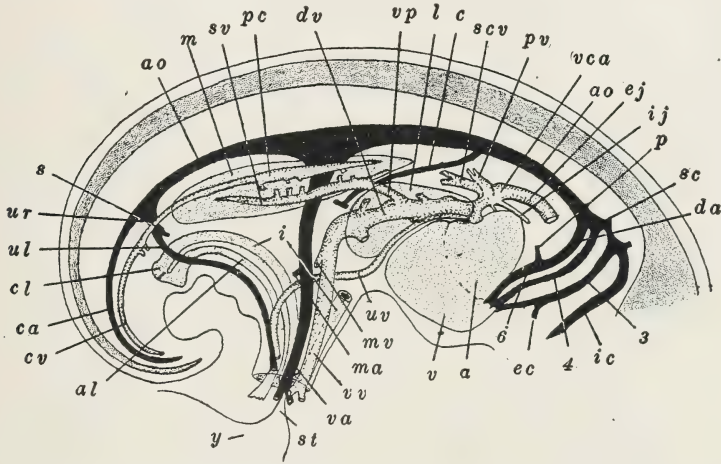


Fig. 297.

Diagrammatic lateral view of the chief embryonic blood-vessels of the chick, during the sixth day. *a*, Auricle; *al*, allantoic stalk; *ao*, dorsal aorta; *c*, celiac artery; *ca*, caudal artery; *cl*, cloaca; *cv*, caudal vein; *da*, ductus arteriosus; *dv*, ductus venosus; *ec*, external carotid artery; *ej*, external jugular vein; *i*, intestine; *ic*, internal carotid artery; *ij*, internal jugular vein; *l*, liver; *m*, mesonephros; *ma*, mesenteric artery; *mv*, mesenteric vein; *p*, pulmonary artery; *pc*, posterior cardinal vein; *pv*, pulmonary vein; *s*, sciatic artery; *sc*, subclavian artery; *scv*, subclavian vein; *st*, yolk-stalk; *sv*, subcardinal vein; *ul*, left umbilical artery; *ur*, right umbilical artery; *uv*, left umbilical vein; *v*, ventricle; *va*, vitelline artery; *vca*, anterior vena cava (anterior cardinal vein); *vp*, posterior vena cava; *vv*, vitelline vein; *y*, yolk-sac; 3, 4, 6, third, fourth, and sixth aortic arches. (From Lillie's "Development of the Chick," by permission of Henry Holt & Co., Publishers.)

mon tube-like entry into the heart is called the **meatus venosus**; the portion nearest the heart is the **sinus venosus**; and the portion lying more distal, the **ductus venosus**.

The dorsal aorta gives off numerous branches supplying various portions of the body of the embryo, the blood being returned by two large veins on each side of the body. That from the anterior part of the embryo is carried through the anterior cardinal veins, and that from the posterior part of the body is carried by the posterior cardinal veins; the anterior and posterior cardinals then unite into a common vein before emptying into the sinus venosus, and this common vein is called the **duct of Cuvier**.

## CHAPTER VIII

### THE DIFFERENTIATION OF THE SOMITES

THE somites have already been described as almost solid triangular blocks of cells derived from the dorsal mesoderm. There is a tiny opening in the center running horizontally through each somite. Oftentimes the opening cannot be seen at all. This opening is called the **myocoele**.

As the embryo continues to increase in size, the triangular block becomes more or less circular and there are two layers of cells, an outer epithelial layer and an inner portion (Fig. 298). The inner portion has its cells irregularly arranged.

It is this ill-defined group of cells which is known as the **sclerotome**. The cells are mesenchymal.

The sclerotomes of each side now grow still farther toward the notochord and surround it. Later they develop into the vertebrae.

The dorsal portion of the outer cell mass whose more medial portion became the sclerotome, has retained its definite outlines and epithelial characteristics. This portion, now called the **dermatome**, is to become the deeper layer of the integument. It is important

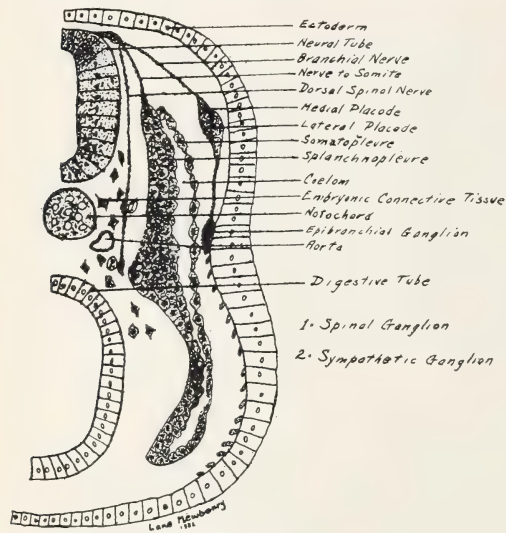


Fig. 298.

Diagram of Myotome and Nerve Development. The more dorsal portion of the somatopleure is known as the dermatome while the dorsal portion of the splanchnopleure lying closest to the dermatome forms the sclerotome.

to remember at this point that the ectoderm gives rise to the epithelial layer of the integument only.

The portion of the cell mass, which lies medial and slightly ventral to the dermatome, is called the **myotome**. The myocoele now lies between the dermatome and the myotome. It is from the myotome that the entire skeletal musculature is developed by the ventral walls of the myotome, becoming converted into longitudinal muscle fibers. These bands of fibres then remain divided into blocks which correspond to the original somites. Here again we have a metameric arrangement of muscles in the embryo of the chick which corresponds to the segmental arrangement of muscles in the adult fish.

The outer portion of the myotome gives rise to the muscles of the neck and trunk. The muscles of the appendages arise independently of the myotomes.

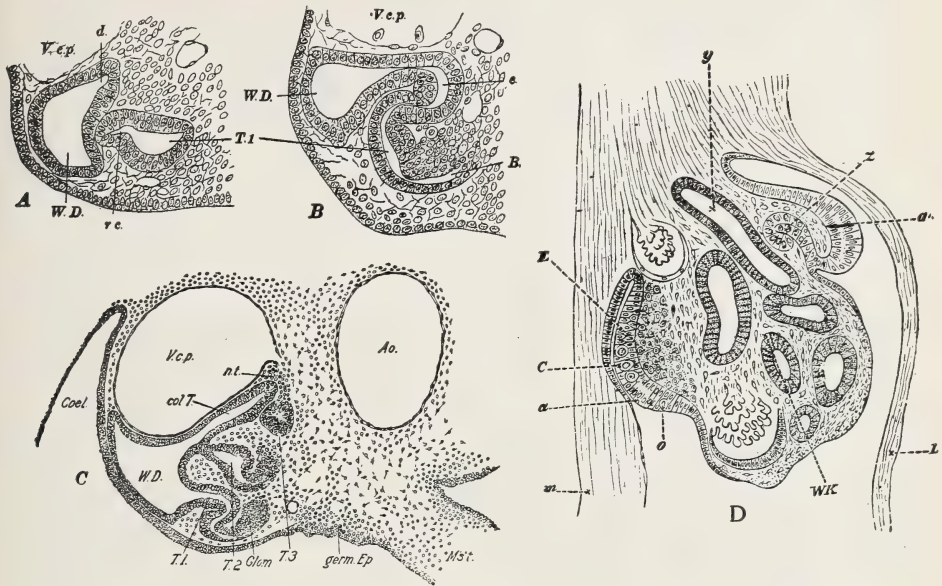


Fig. 299.

The development of the mesonephros. *A, B.* Transverse sections through the mesonephric tubules of the duck embryo with forty-five pairs of somites. After Schreiner. *C.* Transverse section through the middle of the mesonephros of a chick of ninety-six hours. From Lillie (*Development of the Chick*). *Ao.*, Dorsal aorta; *B.*, rudiment of Bowman's capsule; *c.*, collecting duct; *Coel.*, coelom; *Col. T.*, collecting tubule; *d.*, dorsal outgrowth of the Wolffian duct; *Glom.*, glomerulus; *germ. Ep.*, germinal epithelium; *M's't.*, mesentery; *nt.*, nephrogenous tissue; *r.*, rudiment of conducting portion of primary tubule; *T. 1, 2, 3*, primary, secondary, and tertiary mesonephric tubules; *V.c.p.*, posterior cardinal vein; *W.D.*, Wolffian duct. *D.* Cross section through the head kidney in the region of the gonads of a 4 day chick embryo. *a.*, germinal epithelium showing the primary germ-cells *c* and *o*; *a.*, portion of the peritoneal epithelium which forms the Mullerian duct; *E.*, the tissue immediately surrounding the germ cells which forms the stroma of the gonads later; *L.*, Somatopleure; *m.*, mesentery; *WK.*, Pronephros; *y.*, Wolffian duct; *z.*, Mullerian duct. (After Waldeyer and O. Hertwig.)

## THE EXCRETORY SYSTEM

It is on the third day that the intermediate cell mass—the **mesomere** (Fig. 268, mm)—lying between the somite proper and the point where the mesoderm splits into somatic and splanchnic layers, becomes very prominent, being covered with sharply defined epithelial cells (Fig. 299).

It is of great importance for one's future study of embryology as well as for the study of comparative anatomy that the development of the excretory system be thoroughly understood.

It is this intermediate cell mass or mesomere, now called the **nephrotome**, which is to develop into both urinary and reproductive systems.

The Wolffian duct has already been mentioned. The embryonic kidney in the chick is called the **Wolffian body** or **mesonephros**. This embryonic kidney ceases to function very soon after hatching, and is then replaced by the **metanephros**.

One of the lowest forms of a **chordate** (an animal which possesses a

notochord), is the small fish-like **amphioxus** or **lanceolatus**. In this animal a primitive form of excretory system develops and persists throughout the adult life of the animal. It is called a **pronephros**, or **head kidney**. This structure develops in the frog and other amphibia during the embryonic period, but it is followed by the **mesonephros**, or **Wolffian body**, which becomes the permanent kidney of the amphibian. In the chick, as in all amniotes, the mesonephros serves as the embryonal kidney, which is then followed by the development of a **metanephros** or permanent amniote kidney (Fig. 300).

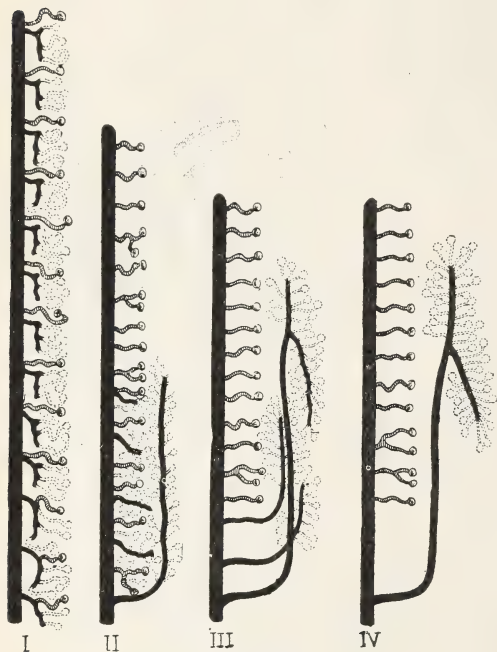


Fig. 300.

Schematic arrangement to show relationship of metanephros and mesonephros. *I*, in *Gymnophiona* (tropical amphibians without tails or legs). *II*, in advanced chick embryo. *III*, one type of its appearance in man. *IV*, in rabbit. The Wolffian duct and ureters are black. The canaliculae of the mesonephros are hatched. The canaliculae of the metanephros are dotted. (After Felix.)

The higher animal forms develop what the immediately lower animal form possesses, plus the next succeeding type of pronephros, mesonephros, or metanephros.

*Amphioxus*, therefore, has the pronephros as its permanent kidney; amphibians have the pronephros as a sort of embryonic kidney with the mesonephros in the adult form; while all higher types of animals have a pronephros (which just appears and degenerates during the early embryonic period) with a mesonephros acting as an embryonic organ of excretion; and then, later, from the caudal region of the mesonephric duct the adult permanent kidney or metanephros develops.

To obtain a clear and accurate view of the functional and structural relations of the three kidney-forms, it is important to summarize the nephridial theory.

Notwithstanding the type of these three kidneys which an animal may possess in adult life, all of the

Theoretically, it appears that the waste matter containing nitrogen, which is elaborated in the primitive liver and collected in the coelom, together with the coelomic fluid itself, passes outward through the nephrostomes and tubules in each segment. In higher forms all the parts are more differentiated and some of the segmentation is lost.

Figure 168 (Vol. I) gives a clear understanding of the earthworm's segmented excretory system which represents the pronephridic type of kidney.

Such a primitive type of nephridia, if completely developed, may be described as follows: At the proximal end of the tubule, a ciliated funnel, the **nephrostome**, opens into the coelom. The cilia may continue into the tubule to produce a current which will carry the coelomic fluid into and through the tubule. The tubule expands into a **Malpighian** or **renal corpuscle**. This corpuscle consists of a vesicle, known as **Bowman's capsule**, one side of which projects into the other, so that the cavity is nearly filled. This inturned portion is the **glomerulus**, consisting of a network of capillary blood vessels, supplied by an artery and drained by a vein. Beyond the Malpighian corpuscle the tubule becomes convoluted, while its cells become glandular. The first convoluted tubule is followed by a straightened portion, forming a simple U shape. The arms of the U form the ascending and descending limbs. The entire U is called **Henle's loop**. Then follows a second convoluted tubule which passes by means of a short connecting tubule into the non-glandular **collecting tubule**. Other groups of similar-formed excretory units enter this same collecting tubule, which then leads into a urinary duct through which the waste matter is carried out of the body.

Various parts of the complete system just described may be missing in different groups of animals. For example, in **Amniotes**, the nephrostomes are never formed, though they are formed in **Ichthyopsida**.

In the pronephros, the Malpighian corpuscle is quite rudimentary and often entirely lacking, and there is also no differentiation into convoluted tubules and Henle's loop.

The renal corpuscles form a sort of filtering apparatus by which water is passed from the blood-vessels of the glomerulus into the tubules near their beginning. This liquid thus serves to carry out the urea, uric acid, etc., which has been secreted by the glandular portions of the walls of the tubules.

A varying number of nephrotomes are formed in different animal forms, and so also a varying number of nephrostomes are formed. Figure 300 will give the student a general idea of how mesonephros and metanephros follow each other and just what their relations are.

The tiny tubules must not, however, be confused with the ducts. The ducts represent the **collecting tubule** described above.

The pronephric tubules grow first and then join the pronephric ducts. Later the mesonephric tubules grow caudad to the pronephric

tubules and join the same ducts. The original pronephric tubules then degenerate, so that now the ducts which were originally called pronephric become the mesonephric ducts.

In the real kidney, or metanephros, the tubules do not grow toward the mesonephric ducts, but **from** these ducts. They grow headward and laterad and ultimately connect with the tubules of the mesonephros, after which the mesonephros itself degenerates with the exception of the Wolffian or mesonephric ducts, which in the male become the tubules through which the sperm pass.

With this in mind, the excretory system of the chick can be studied with some understanding.

At about thirty-six hours, it will be remembered, the pronephric tubules were seen to arise from the nephrotome, one pair lateral to each somite from the fifth to the sixteenth. Each tubule arises as a solid bud of cells with the free ends growing dorsad, close to the posterior cardinal veins. The distal end of each tubule is bent caudad later, until it reaches the tubule directly posterior to it. Thus is formed a continuous cord of cells, which is to become the pronephric duct. These ducts continue to extend caudad beyond the region where the tubules were formed, and soon develop a lumen. The ducts ultimately reach the cloaca, extending ventrally and opening into it.

The best way to study a series of cross sections is to begin caudad and observe them serially toward the head, because the posterior portions are not so well developed as are the anterior.

The pronephros (Figs. 285 and 299, D) varies in its development, although it usually can be noted in from the fifth to the fifteenth or sixteenth somite. Typically it develops from the tenth to fifteenth, inclusive. No duct is formed anterior to the tenth somite, but the pronephric buds in that region disappear by the end of the second day.

Mesonephric tubules (Fig. 299, A, B, C), develop in all segments from the thirteenth or fourteenth to the thirtieth, so that the most anterior mesonephric tubules develop in the same segments where the pronephric tubules also developed, although it is only posterior to the twentieth segment that the mesonephros develops **typically**.

The mesonephric tubules, which are to connect with the ducts, are developed from radially arranged cell masses lying ventral and medial to the ducts. The most anterior of these tubules acquire a lumen by the time the ducts have developed their lumen. These tubules grow toward and connect with the duct. Later they remain as isolated vesicles. The grouping of the mesonephric tubules constitutes the **mesonephros** or **Wolffian body**. Some of the more cephalad mesonephric tubules seem to develop nephrostomes opening into the coelom.

The tubules themselves, having formed separately from the ducts and then grown outward and connected with them, have had their outward ends develop a cluster of closely packed cells which lies in close

relationship to the dorsal aorta. This cluster becomes the glomeruli. In fact, by the fifth day, circulation has already been established in the glomeruli, and from then until the eleventh day, the mesonephros is at the height of its functional activity. Then the metanephros takes its place.

The pronephric tubules, which attain even a degree of completeness, lie in the tenth to fifteenth somites. It is interesting to observe that it is when these tubules begin to degenerate that the glomeruli begin to form at the points of the tubules, close to the coelom and actually project into the coelom. These bud-like structures are extremely variable, both as to number and degree of development. They even develop differently on both sides of the chick. They appear to be best developed on the third and fourth days. It is for reasons such as these that former writers insisted that, in the chick, the pronephros really developed **later than** the mesonephros.

# CHAPTER IX

## THE DEVELOPMENT OF THE FOURTH DAY

UPON opening an egg which has been incubated for four days, the great increase in size of the embryo is the most noticeable feature. The germinal membrane now covers almost one-half of the yolk, and the vascular area is very prominent, although the sinus terminalis has already begun to diminish in distinctness.

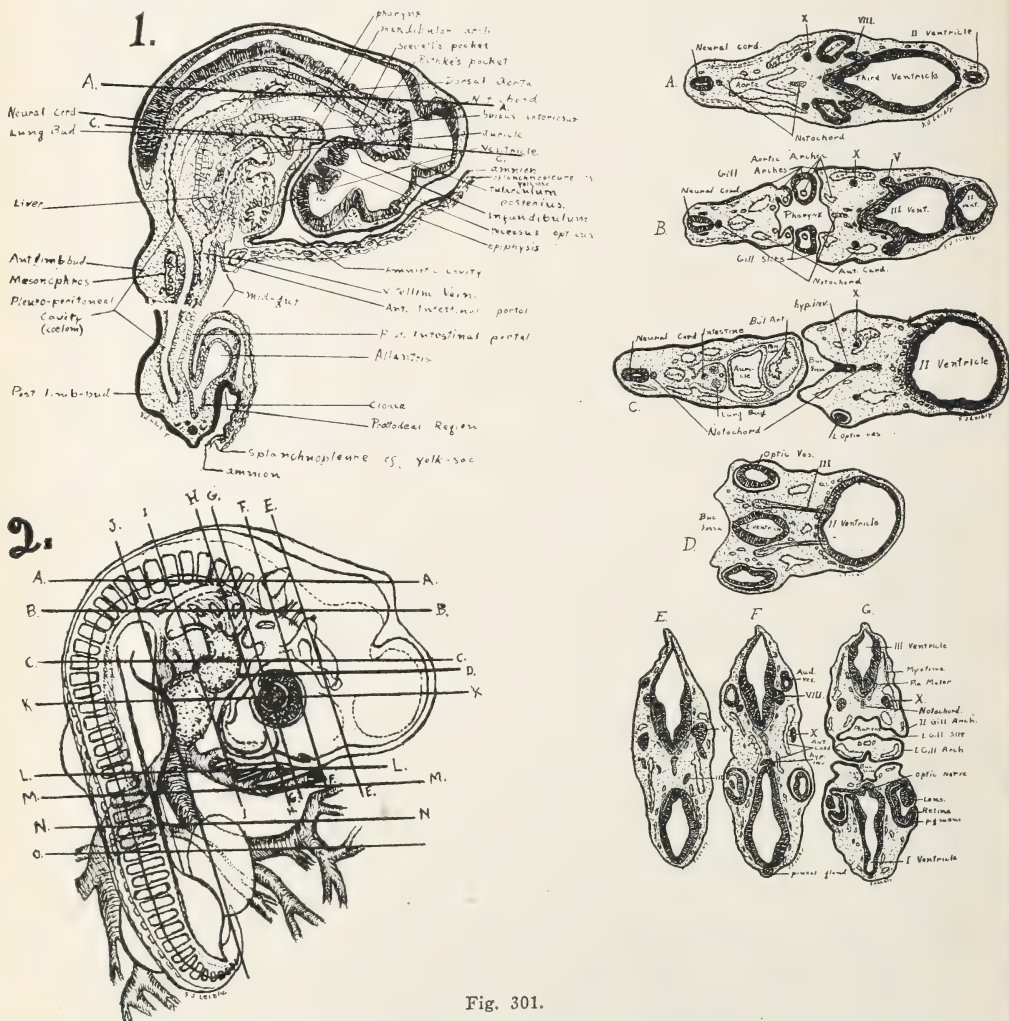


Fig. 301.

1. Median sagittal section of 82 hour chick embryo. 2. Whole mount to show regions from which A to O are cut. Sections A=A-A; B=B-B; etc. (Re-drawn from Duval.)

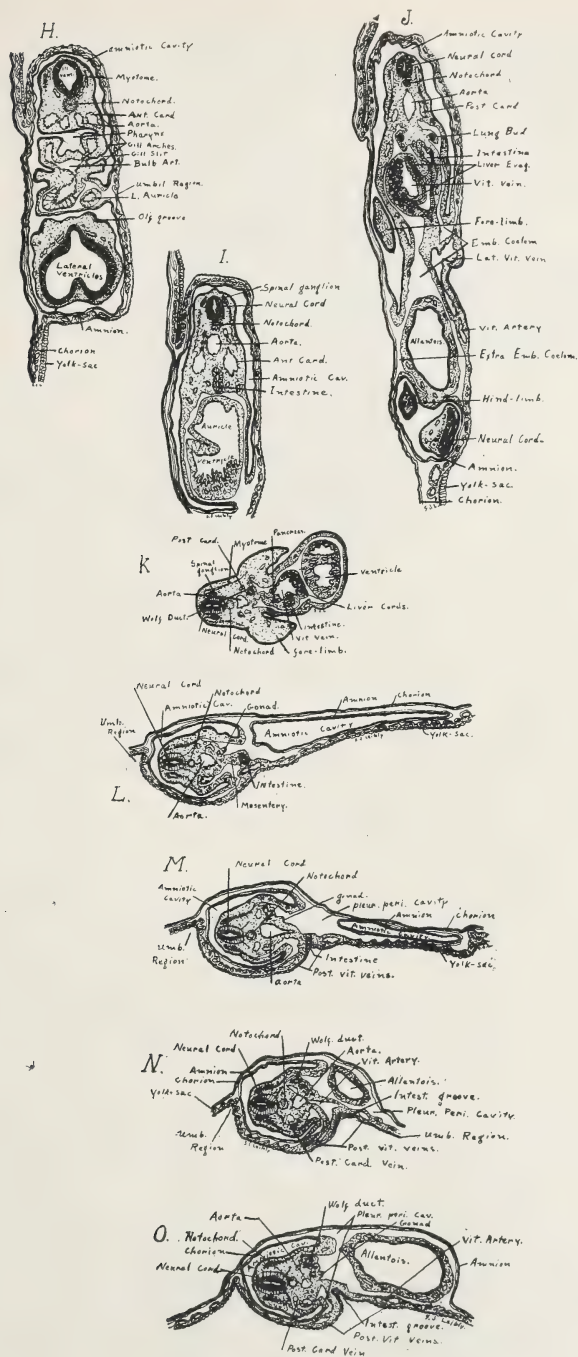


Fig. 301.

The amnion covers the entire chick, but as there is as yet little fluid in the amniotic cavity, the amnion lies close to the embryo.

The splanchnic stalk forms a narrow tube, connecting yolk-sac and mid-gut, but the somatic stalk has not kept even pace with the splanchnic, so that there is a ring-shaped space between the two through which the allantois projects. The allantois is connected by a narrow stalk with the hind-gut just cephalad to the tail.

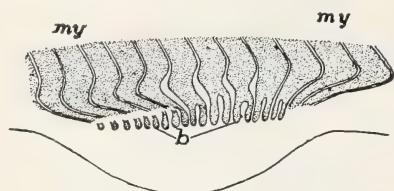


Fig. 302.

Appendage muscles being budded off from myotomes in the European Dogfish, *Pristiurus*. *b*, muscle buds; *my*, myotomes. (From Kingsley after Rabl.)

point of separation the somatopleure is raised to form a longitudinal ridge on each side, which is called the **Wolffian ridge**.

It is on this day also that the beginnings of the appendages, the wings and legs, can be seen as local swellings of the Wolffian ridge.

These arise (the wing-buds just posterior to the heart region, and the hind-limb-buds just anterior to the tail) as conical or triangular groups of mesoderm (Fig. 302) covered by ectoderm. By the end of the day the wing-buds have become elongated and narrow, while the limb-buds are short and broad.

The embryo now lies on its left side, torsion being complete to the extent of ninety degrees.

It is on this day also that a fourth gill cleft appears. The gill arches become so thick now that one can scarcely see the aortic arches in any of them.

In the head region, the cephalic flexure presses the ventral surface of the head so tightly against the pharynx that the head and pharyngeal region must be removed and studied from their ventral aspects or little can be observed.

Figure 296 will show that the mandibular arch forms the more caudal boundary of the oral depression, while on each side, the arch forms an elevation, the maxillary processes, which grow mesiad and form the antero-lateral boundaries of the mouth opening.

The nasal pits form as hollow depressions in the ectoderm of the anterior part of the head overhanging the mouth region with U-shaped elevations surrounding them. The median limb is the **naso-medial process** and the lateral limb is the **naso-lateral process**. The two naso-medial processes grow toward the mouth and meet the maxillary

The cranial flexure increases to a considerable extent as does also the body flexure, so that the embryo now describes a half-circle.

The muscle plates are nearly vertical in position, extending almost to the point of separation of somatopleure and splanchnopleure, while just beyond this

processes which grow inward from each side. It is the fusion of these two naso-medial processes with each other in the midline and with the maxillary processes laterally that forms the upper jaw, the **maxilla**.

The lower jaw is formed by the fusion in the midline of the right and left portions of the mandibular arch.

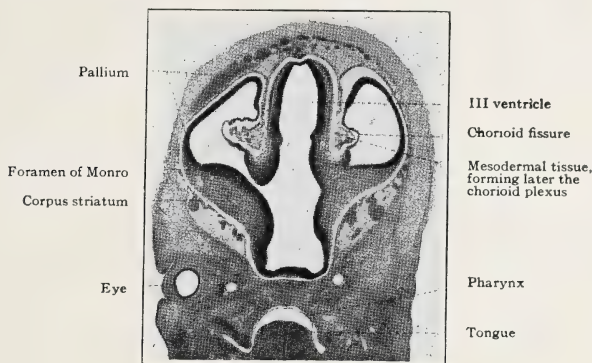


Fig.303.

Transverse section through the forebrain of a 16 mm. human embryo (six to seven weeks) to show the relationship of the ventricles.

## THE NERVOUS SYSTEM

Figures 282 and 288 show how the two lateral evaginations of the fore-brain stand in relation to the cephalic end of the central nervous system, and why it is that the ears come to lie on practically the same dorso-ventral level with the eyes, although they begin forming so far apart.

The development which brings this about has already been discussed. Here it is important for the student to observe that the two evaginations, forming the telencephalic vesicles, have an open space within them, known as the I and II ventricles—also called **lateral ventricles**. The portion between them is the III ventricle, which is later to become a mere connecting slit-like tube to connect the lateral and more posterior ventricles. The entire opening in the fore-brain is called the **telocoele**; that in the diencephalon, the **diocoele**; that of the mesencephalon, the **mesocoele** (later called the **aqueduct of Sylvius**); that of the metencephalon, the **metacoele**; and that in the myelencephalon, the **myelocoele**.

Figure 282 also shows that what was once the most anterior part of the fore-brain, i. e., the lamina terminalis, is no longer so, the lateral vesicles having extended further forward. The telencephalic vesicles become the cerebral hemispheres in the adult. These become so large that they cover the entire diencephalon and mesencephalon.

All discussion of the central nervous system in our future study of

comparative anatomy will depend upon the student's thorough understanding of the development of the brain regions and vesicles as here discussed. Consequently, the various arbitrary lines used as demarcations must be carefully studied.

The division between telencephalon and diencephalon is the imaginary line drawn from the **velum transversum** to the **recessus opticus**. The velum is that slight extension marking the point where the primary fore-brain is to divide, while the recessus is that transverse furrow in the floor of the brain, which leads directly into the lumina of the optic stalks.

**The Diencephalon:** There is little change in this on the fourth day, except that the infundibular depression in the diencephalon has deepened, and lies close to Rathke's pocket (Fig. 301, I), with which it later fuses to form the **hypophysis**. Later the lateral walls of the diencephalon are to become thickened to form the **thalami**. As these thalami grow inward toward each other, they will cause the diocoele, or third ventricle, to become quite small. The anterior part of the roof of the diencephalon remains thin, and the blood-vessels grow downward into the diocoele as the **choroid plexus**.

The division between diencephalon and mesencephalon is an imaginary line drawn between the **tuberculum posterius** (a rounded elevation in the floor of the brain, of importance only as a landmark of this kind), and the internal ridge formed by the original dorsal constriction between the primary fore-brain and mid-brain.

**The Mesencephalon:** There is little change in this portion of the brain, though a little later, dorsal and lateral walls become thickened to form either the **optic lobes** or the **corpora quadrigemina**. Optic lobes and optic vesicles must not be confused, as these are two separate and distinct structures.

The floor of the mesencephalon thickens to form the **cerebral peduncles** of the adult, which serve as the main pathway for the fiber tracts which connect the cerebral hemispheres with the posterior part of the brain and spinal cord. The mesocoele becomes quite small by these various thickenings and is now called the **aqueduct of Sylvius**.

**The Metencephalon:** The metencephalon is separated from the mesencephalon by the original inter-neuromeric constrictions which arose early and marked off this portion of the brain. The caudal boundary is not well defined, though it is supposed to merge in the myelencephalon where the roof changes from its thickened state to the thinner condition observed more posteriorly. There is little change on the fourth day in this region, though later an extensive ingrowth of fiber tracts develops both on the ventral and lateral walls. These fiber tracts form the **pons** and the **cerebellar peduncles**, while the roof of the metencephalon enlarges to become the **cerebellum**.

**The Myelencephalon:** There is also little change in this region, but

later the roof becomes thinner, and blood-vessels push their way into the opening now called the fourth ventricle, as the **posterior choroid plexus**, while the ventral and side-walls become floor and lateral walls of the medulla.

### THE GANGLIA OF THE CRANIAL NERVES (Fig. 282, B)

Along the neural crests already discussed, various ganglia are formed. The largest on the fourth day is known as the **Gasserian ganglion** of the **fifth cranial nerve**. (The fifth is also called the **trigeminal nerve**.) It lies ventral and lateral, as well as opposite to the most anterior neuromere of the myelencephalon. It forms the **sensory nerve fibers** which grow from the brain mesially and distally into the mouth and face region. This fifth cranial nerve is divided into three great branches: the **ophthalmic**, the **maxillary**, and the **mandibular**.

The first branch, the ophthalmic, can be seen on the fourth day extending toward the eye, while the other two are just beginning to grow toward the mouth angle.

Just anterior to the auditory vesicle a mass of neural-crest cells is developing into what is to become the **facial** or **seventh cranial nerve** and the **acoustic** or **eighth cranial nerve**. This cell mass divides on the fourth day to form the **geniculate ganglion** of the seventh and the **acoustic ganglion** of the eighth nerve.

Caudad to the auditory vesicle, the ganglion of the **glossopharyngeal** or ninth cranial nerve can be seen, and the ganglion of the vagus or tenth nerve may just be observed. The ninth can be seen in whole mounts, the tenth probably cannot.

### THE SPINAL CORD

Throughout the spinal cord there is a compressed slit-like lumen known as the **central canal**. Just as the ganglia of the cranial nerves make their appearance on the fourth day, so, too, do the spinal nerves.

It requires special methods of staining to study the growth of the nerve fibers from the **neuroblasts**, but the development of the spinal nerve roots can be studied in ordinarily stained slides.

It is important to understand that in the adult there will be two roots to each spinal nerve (Fig. 290), one **ventral**, which is **motor** in function, and one **dorsal**, which is **sensory** in function. Both of these unite lateral to the spinal cord. Immediately distal to this union there is a branch extending to the sympathetic nerve cord. This branch is known as the **ramus communicans**, and extends ventrad.

Before the union of dorsal and ventral nerve roots takes place, a **spinal ganglion** or **dorsal ganglion** is seen lying in the dorsal roots. This ganglion is formed from the neural crests, and grows toward the cord, thus forming the dorsal root, but there are also fibers growing away

from the cord from this same ganglionic region which are known as **peripheral nerves**.

The ventral roots (Fig. 290) are formed by fibers growing out **from** the lateral portions of the cord itself, and are thus **efferent** nerves carrying motor impulses from the brain and spinal cord to the muscles.

The **sympathetic ganglia** (Figs. 268, 290, 298) arise from cells which have migrated ventrally from the neural crests to form cell masses on each side of the midline on a level with the dorsal aorta. They are connected to form cords, and on the fourth day enlargements can be seen on these cords opposite the dorsal ganglia. These enlargements are the **primary sympathetic ganglia**, each one of which is connected by a **ramus communicans** to the corresponding spinal nerve. Later, both sensory and motor fibers will extend to the sympathetic ganglia from the spinal nerve roots as **rami communicantes**, while fibers running out from the sympathetic ganglia connect with the various organs of the body.

## THE ORGANS OF SPECIAL SENSE

### THE EYE (Fig. 289)

We have already discussed the projections from the fore-brain which are to form the optic cups as well as how the ectoderm directly opposite the optic cup thickens to form the lens, this lens then meeting with the cup.

On the fourth day the beginning of almost all the adult structures of the eye can be seen.

The thickened internal layer of the optic cup will give rise to the sensory layer of the retina.

The fibers which arise from the nerve cells in the retina grow along the groove in the ventral surface of the optic stalk toward the brain to form the optic nerve.

The external layer of the optic cup will become the pigment layer of the retina.

About the inside of the optic cup a grouping of mesenchymal cells can be seen which gives rise to the sclera and the choroid coat.

Some of the mesenchymal cells even make their way into the optic cup through the choroid fissure and give rise to the cellular elements of the vitreous body.

From the margins of the optic cup closest to the lens, the ciliary apparatus of the eye is derived.

From the superficial ectoderm which overlies the eye, the corneal and conjunctival epithelium are derived.

The mesenchymal cells which migrate to the region between the lens and the corneal epithelium give rise to the **substantia propria** of the cornea. The lens forms as a thickening of the superficial ectoderm, which then becomes depressed so that it forms an invagination into the

optic cup. The margins of the cup narrow and converge toward the lens, while the lens itself loses its connection with the superficial ectoderm and forms a completely closed vesicle. A microscopic study of sections of the lens show an elongation of the cells on that side of the lens which lies toward the center of the optic cup. These elongating cells are to become the **lens fibers**.

### THE EAR

The auditory placode has already been mentioned as forming on the second day. This thickening of the ectoderm sinks below the surrounding ectoderm and becomes the floor of the auditory pit. This separates from the superficial layer from which it formed. It will be remembered that this causes the auditory pit to lie close to the myelencephalon. The tubular connection formed by the constriction of the region between the sunken placode and the superficial layer where it originally forms, remains open for a time as the **endolymphatic duct**.

It is by a series of complicated changes that this placode, which forms a vesicle, gives rise to the entire epithelial portion of the **internal ear** mechanism.

Nerve fibers from the **acoustic ganglion** grow **inward to the brain** and **outward to the internal ear**, thus forming its nerve connections. The external auditory meatus cannot yet be seen, nor has the dorsal and inner part of the hyomandibular cleft as yet given rise to the Eustachian tube, which is to form later.

### THE NOSE (Fig. 304)

The olfactory pits are merely paired depressions in the ectoderm of the head, ventral to the vesicles of the fore-brain, and just anterior to the mouth. These pits become deepened by the growth of the surrounding parts. The epithelium of the pits ultimately comes to lie at the extreme upper part of the nasal chambers, and there constitutes the **sensory epithelium**. Nerve fibers grow inward from these cells to the lobes of the fore-brain, constituting the **olfactory** or **first cranial nerves**.

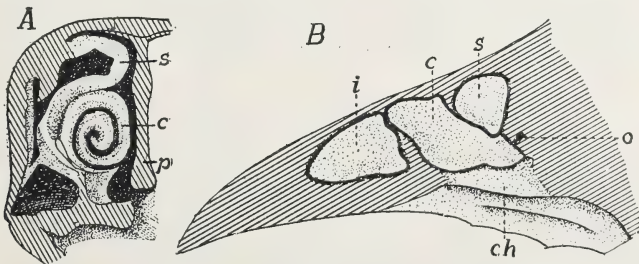


Fig. 304.

Olfactory region of the hen, *A* in transverse and *B* in longitudinal section. *c*, middle concha; *ch*, choana; *i*, inferior (anterior) concha; *o*, connection of air cavity with head; *p*, septum of nose; *s*, superior concha. (From Kingsley after Gegenbaur.)

## THE SKELETAL STRUCTURE

On the fourth day the mesoderm surrounding the brain has increased and begins to show slight traces of the skull formation toward the anterior portion of the head, and to extend posteriorly. The **fronto-nasal process** has already been discussed as well as the formation of the upper and lower jaws.

The beginnings of the vertebral column are also in evidence, though only to a slight extent. Nevertheless, it is well at this point to summarize what will occur, so that future changes will be understandable.

During the fourth day the somites have increased from about thirty to forty. Each somite now shows a more or less distinctive division into an outward lying **muscle plate** and an inner region which is to form the vertebral column. It is from these inner portions that processes of mesoderm are sent out by both dorsal and ventral regions to the neural canal, as well as below the notochord, until these structures are com-

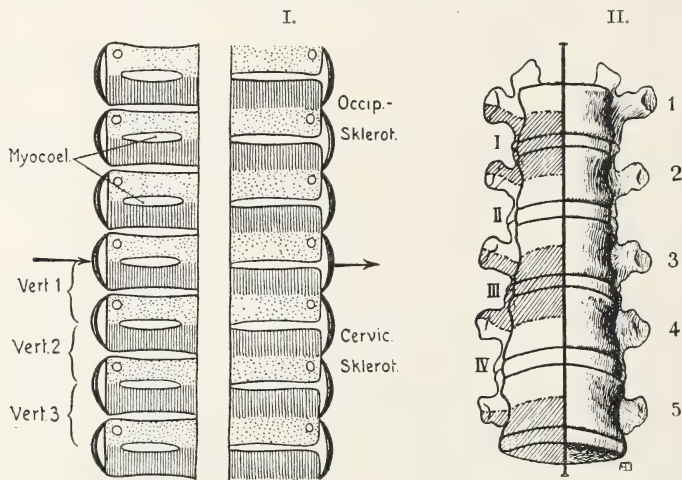


Fig. 305.

I, Redividing of the spinal segments. On the left side of the cut the sclerotomes and myotomes are seen in their original state. On the right they are seen in their final state. The cephalic portions are dotted and the caudal portions hatched. The arrows show the line of demarcation between head and neck. II, Ventral view of spinal column to show redivided parts of each vertebra. (From Corning, after Kollmann.)

pletely surrounded by mesoderm. By the end of the fourth day these processes have become thickened, and are often called the **membranous vertebral column**. The membranous vertebral column is still segmented, each segment corresponding to the original somite from which it sprang.

On the fifth day these lines of segmentation disappear in the mesoderm which becomes continuous in its surrounding of the neural canal and notochord, though the muscle plates retain their segmentation.

On the fifth day also, the mesoderm lying in immediate contact with the notochord becomes cartilaginous, to form a cartilaginous sheath

around the notochord throughout its entire length, while at each side of the spinal cord, paired bars of cartilage form, which will shortly fuse with the cartilaginous sheath of the notochord to form the beginnings of the neural arches.

Toward the end of the fifth day the points opposite the attachment of the neural arches become thickened and more mature, but the portions between the neural arches retain their embryonic character. This causes what has been called a **secondary segmentation** of the cartilaginous tube. Later this segmentation becomes still greater until the entire cartilaginous tube is made up of a series of vertebral rings or segments, each segment consisting of a vertebral ring with its attached neural arch, and the anterior-posterior halves, respectively, of the succeeding and preceding intervertebral rings. Each of these segments becomes one of the vertebrae which constitute the spinal column.

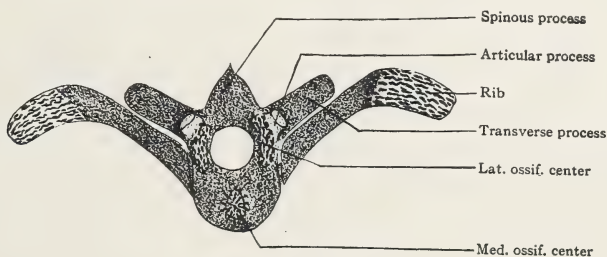


Fig. 306.

Thoracic vertebra and ribs of human embryo of 55 mm. (Middle of 3rd month) to show ossification centers. Cartilage is indicated by stippled areas, and ossification centers by irregular black lines. (After Kollmann.)

It must be understood, however, that these so-called secondary segments do not correspond with the somites from which they were formed. The secondary lines of segmentation lie at about the center of the muscle plates (Fig. 305), so that each of these secondary segments obtains approximately one-half of the muscle action from the immediately anterior muscle plate, and one-half from the immediately posterior muscle plate, thus making it possible for each one of the vertebrae to have the muscles from the two regions act upon it.

The spinal column develops around the notochord.

Ossification of the vertebrae begins about the twelfth day in the **centrum** of the second or third cervical vertebra, gradually extending caudad. The neural arches ossify still later in two **centers of ossification**. (Fig. 306.)

On about the seventh day, the centrum of the first cervical vertebra, or atlas, separates from the rest of the bony ring and becomes attached to the axis to form the **odontoid process**.

On the seventh day there are present about forty-five vertebrae.

The most posterior five or six fuse a little later and form the **pygostyle** (Fig. 418).

## THE EXCRETORY SYSTEM

The anterior tubules of the Wolffian body disappear before the end of the fourth day, while the posterior tubules have increased in size and become convoluted. The intermediate cell mass from which they arise is quite prominent. In cross-sections the convoluted tubules will naturally be cut at all angles, but they can be distinguished from the duct by observing their much thicker walls. The glomeruli can also be seen filled with blood vessels.

The permanent kidney, or metanephros (Fig. 307), begins its

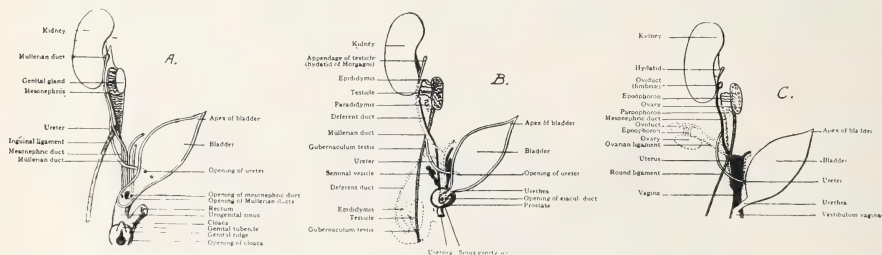


Fig. 307.

Diagram of Urogenital Organs. *A*, in indifferent stage. *B*, development of the male from the indifferent Anlagen, and *C*, development in the female from the indifferent Anlagen.

The dotted lines represent the organs in their relative positions in the adult stage with the exception of the Müllerian duct in the male and the mesonephric duct in the female. These latter ducts disappear for the most part. (After Hertwig.)

development toward the fourth day in the region lying between the Wolffian body and the cloaca, that is, between the thirtieth and thirty-fourth segment.

The metanephric duct, or **ureter**, forms first, as did the ducts of the pronephros and the mesonephros. This duct grows forward on the outer side of the mesoderm lying in the region just mentioned. It grows from the dorsal side of the posterior end of the Wolffian duct anteriorly. Naturally it has an opening into the Wolffian duct from which it is a diverticulum, but on the sixth day it develops a separate opening into the cloaca.

It is from these ureters that lateral outgrowths arise, which join with the rods of tissue now forming in the surrounding mesoderm. These outgrowths then develop into the tubules and Malpighian bodies of the metanephros in a similar manner to the way the Wolffian bodies developed.

The permanent kidney is quite small when compared with the mesonephros, but it increases in size to a considerable extent just before hatching.

**THE REPRODUCTIVE SYSTEM (Fig. 307)**

On the fourth day a thickened strip of peritoneum forms on the lateral and superior face of the Wolffian body, which later extends all the way to the cloaca. This may be called the **tubal ridge**. It appears first at the anterior end of the Wolffian body and grows posteriorly, immediately external to the Wolffian duct. This tubal ridge invaginates to form a groove-like arrangement at the cephalic end of the Wolffian body. The lips of this groove then fuse to form a tube—the **Müllerian duct**. Fusion takes place on the fifth day. The anterior end of this Müllerian duct remains open in the coelom. The Müllerian duct becomes the oviduct. There are several openings which will develop at the anterior end in addition to the main one, but these latter close normally. Should they remain open, the abnormal condition of having two openings in the duct results in the adult stage. The posterior end remains closed.

The older embryologists considered these two or three openings in the Müllerian duct as homologous with the nephrostomes of the pronephros, and so insisted that the pronephros followed the mesonephros in the chick. Modern embryologists consider that these openings lie entirely too far posteriorly and laterally to permit of this older interpretation.

In both sexes so far development has been alike, but on the eighth day the Müllerian ducts begin to degenerate in the male. They disappear almost entirely by the eleventh day.

In the female chick, the left Müllerian duct forms the oviduct, while the right Müllerian duct degenerates. The left one alone remains functional.

The Wolffian body disappears almost entirely in the male, though a small group of tubules, covering the anterior head of the testes, remains as the **epididymis**. In the female it also disappears almost entirely, the part remaining being the **parovarium**, a small body lying in the mesentery between the ovary and the kidney.

The Wolffian duct disappears entirely in the female but acts as the **vas deferens**, or sperm duct, in the male.

The germ cells probably arise from the entoderm in vertebrates. The entoderm is never metameric, though some of the older embryologists spoke of metameric **gonotomes** as primitive segmented regions which were to form the gonads.

At about the time the somites form, the portion of the entoderm which is to become the gonads, migrates through the developing mesoderm in the epithelium of the genital ridges which have formed immediately lateral to the mesentery. The primitive or **primordial ova**, or sperm, can be recognized not only from their size but from their reactions to microscopic stains (Fig. 254).

In the female, the epithelium increases in thickness to an enormous extent. The primitive ova multiply, and the products of this multiplication, accompanied by some of the epithelial cells, sink into the deeper stroma of the connective tissue, and thus form **ovarial** or **medullary cords**, each such cord containing a number of ova. The cords then break up and each egg becomes surrounded by a layer of epithelial cells, the whole forming a **Graafian follicle**. The follicle cells supply the nourishment to the egg lying within.

This whole growth takes place only on the left side of the chick, as the right ovary is not functional.

In the male, the beginnings of the gonad formation are similar to that of the female; but instead of the cords breaking up into separate follicles, each cord develops a lumen which becomes converted into the **seminiferous tubule**. One can, however, see in the walls of these tubules both types of cells that were seen in the Graafian follicle. Indeed, there is found a third type of cell called **Sertoli's cell**, which is supposed to act as a sort of nutritive or **nurse cell** to the developing sperm.

### THE ADRENAL BODIES

While these bodies lie closely attached to the kidney, they have not developed as a part of the urinary system.

It is important to know that the adrenal organs, which are among the prominent ductless glands now studied in the schools, arise from two separate and distinct origins:

First, by a proliferation of peritoneum, and second, by a proliferation of the sympathetic ganglion cells. It is the portion arising from the peritoneum which connects with the mesonephros.

The peritoneal proliferations begin as cords, or strands of cells, along the dorsal aorta. These then connect with the renal vesicles of the mesonephros. Later, the sympathetic proliferations extend within the peritoneal cords, so that the peritoneal cords now become the **cortex** and the sympathetic portions become the **medulla** of the adult adrenal glands.

### THE CIRCULATORY SYSTEM

At this point it is well for the student not only to realize, but to appreciate the great number of experiments necessary to demonstrate biological facts, as well as to understand the great number of possible errors and objections which men may bring forth to oppose the interpretation of these facts after the facts themselves have been demonstrated.

Suppose the question were raised whether the first beating of the heart of an embryo is muscular or nervous in type. What experiments, for example, would be necessary to answer such a question satisfactorily?

Off hand, one might say that, as nerves carry impulses to all muscles and as there are nerves in the heart muscle, the action must be nervous.

Nerve fibers grow into the heart muscle from the nerve cells close by, but the very finest nerve stains known, have been unable to demonstrate that there are any nerves whatever in the heart muscle at the time of its earliest beating. It may be objected that, however fine our nerve stains may be, they are not sufficiently so to demonstrate **possible** nerve cells or parts of nerve cells. And that, if we improve in our technical ability by obtaining new stains, we may expect to find nerve-cell-substance heretofore unseeable. This objection is not well taken because, if any muscle be removed from the body and placed in normal salt solution, the muscle fibers do not lose their contracting ability, although in a few days the nerves degenerate and can be dissected out. If, then, our present stains do show the nerve fibers clearly in embryos, and these can be seen to be in exactly the same position as in the adult heart, as demonstrated by the experiment just cited, it is quite reasonable to assume that the stains do show **all** the nerve fibers that are actually present. If this be true, we can demonstrate that all such nerve fibers, which normally take a stain, have been destroyed. **But, the new nerveless muscle still contracts and expands.**

It could, of course, be argued, in so far as this is embryonic material not yet far removed from the germ plasm, that, therefore, every particle of the embryonic material still retains some of the undifferentiated nerve cells, and consequently every part of the embryo does actually retain some slight nervous substance which may, under extraordinary circumstances, be brought forth.

This objection is overcome by an experiment performed some years ago by taking a portion of the adult intestinal tract, chopping it up very finely, and placing it in a test tube. Notwithstanding the fact that it was thoroughly chopped up, this substance still was able to digest food placed in the tube with it. Those who insisted that all action is nervous in type, then contended that the different particles of the intestine still retained some of the essential parts of the nerve cell, so that, notwithstanding the fact that the parts had been cut up into very tiny particles, the essential nervous elements were still doing the work.

A portion of intestine was then kept in a chemical medium similar to that mentioned in the heart-experiment, and, as with the muscle-experiment, the nerves degenerated and were dissected out, although the intestine itself continued performing its normal functions.

If the tough adult nerve-structures are so easily degenerated in a normal salt solution, it is surely safe to assume that the hundred-fold more delicate embryonic nerve structures will also be destroyed in such a medium.

It will be remembered that the heart grows as a simple straight tube, and that the blood is formed in the blood-islands by the cavities flowing together. As these cavities fuse they become tubular, forming the vitelline veins which carry the blood to the heart.

It is of the utmost importance to remember that this early heart tube, even before the blood passes through it, has a slow, irregular "beat." This, however, is not a true heart-beat but merely the functional movement of living muscle.

The true heart-beat is established at that particular moment when the thin membrane which separates the anterior from the posterior portion in the tubular heart breaks through by the greater pressure of the blood from the posterior region pressing forward. The tiny membrane can be seen to bulge out toward the head region until it finally breaks.

From that moment on, the blood forces its way through the heart and begins a rhythmic muscular reaction on the part of the heart.

The architecture of all muscles is such that various muscle cells are antagonistic to other muscle cells in the same group, so that each muscle can, if it elongates, also contract and shorten, the two sets of fibers being mutually antagonistic, so as to retain a normal balance. The heart muscle shows this principle admirably in that it is composed of two groups of spirally wound muscle fibers, the one unwinding as the other winds up, thus causing a mutual interaction which keeps up by the rhythm of the heart-beat.

From the study of physics we know that, when two streams which run in different directions meet, a **vortex** is formed. If we now turn to our earlier description of the development of the circulatory system during the first two days, we shall find that there are two openings into the heart from which streams of blood are brought into that organ. As these two blood vessels send their streams together a vortex is formed. We thus find a physical explanation as to why the heart muscles follow in their growth the optimum stretching caused by the spirally running stream of blood.

From all that has been said above, it follows that when a heart is removed from an animal body and kept "alive" for days or weeks, it is but the physical continuation of the normal muscular antagonistic reaction of the two spiral shaped groups which have been wound up quite as a clock is wound.

As months and years have elapsed in the winding of these spiral muscles, it is quite natural to understand that they are still sufficiently wound when removed from the body so that they will continue in action for some days if no external conditions exist to cause a stoppage sooner. Such external conditions may be pressure, friction of various kinds, or a drying up of the tissues when not retained in proper media.

If the immediately preceding paragraph be remembered, one can

always explain such objections as this: "If potassium is removed from the medium in which a heart is placed, it ceases to function, thereby proving that it is the potassium solution which causes the reaction." It will be remembered that it was stated in the preceding paragraphs that the action of the muscles will continue for some time until external conditions cause a stoppage. The removal of potassium solution from the surrounding medium has nothing to do with the reaction ability in the muscle cell itself, but its removal removes a factor necessary to reaction, by making the **medium** one in which it cannot react. An example may make the matter clearer. A living human being has the power to move his arms and walk about. This power is retained for many years. Let us suppose that we remove certain substances from the air which are needed for his lungs to function. An individual breathing such an atmosphere would either slowly or rapidly (depending upon what gases are removed) grow less and less able to move his arms or to walk, and in a short time this ability would cease entirely. In other words, such an individual needs a certain kind of atmosphere for breathing purposes, without which he cannot perform his normal functions. This, however, is vastly different from saying that the constituents of air are the cause of his being able to move.

From what has been said above, all that we can say, in regard to nerve-and-muscle-action, is that experiments tend to demonstrate that muscle cells **have the ability to act and react**, and that the **nerves are only the connectors and impulse carriers**, by which a coördination of muscle cells, which are not in contact with each other, may be brought about.

In the embryo, the yolk is converted into blood, and the pressure of that blood as it passes through the various vessels with its greater posterior and its less anterior pressure, brings about the results mentioned above. In the adult, the food that is taken in and converted into blood, works on quite similar principles by continuing to produce a greater posterior than an anterior pressure.

The embryonic circulation can only be understood when it is realized that it varies from the adult circulation in a manner that is accounted for by the difference between embryonic and adult feeding. In the embryo, due to the fact that the food comes entirely from the yolk, there is developed a **yolk or vitelline-circulation**. As the chick's lungs are non-functional before birth, and the allantois functions as a respiratory organ, there is developed an **allantoic circulation**, while a third type is the circulation of the embryo itself. The vitelline and the allantoic together constitute the **extra-embryonic circulation**.

All food material to the embryo comes from the yolk (although the yolk particles do not turn directly into blood. It is the action of the entodermal cells which line the yolk-sac and pour out a secretion of

enzymes, which breaks down the yolk granules). It is thus seen that it is the vitelline vessels which carry food into the embryo, and it is the allantois which serves both as a respiratory and excretory organ (at least until the nephroi are formed). It is the allantoic circulation which permits the escape of carbon dioxide and other waste matters.

Therefore, the intra-embryonic circulation has nothing to do with either manufacturing blood or throwing out waste matter (until the nephroi are formed); it serves only as the **carrier, distributor, and collecting system** of both food and waste materials.

As all three systems, **intra-embryonic, vitelline, and allantoic** send their vessels to and from the heart, the contents of all three systems mingle in that organ, although, of course, the vitelline circulation is the richer in food material, and the allantoic the richer in waste matter.

It is at this point that the student must again remember that arteries need not necessarily carry blood rich in food matter, but that an artery is any blood-vessel carrying blood **away** from the heart under a high pressure. This pressure probably accounts for the fact that arterial walls are thicker and stronger than venous walls.

Veins are the carriers of blood to the heart.

### THE VITELLINE CIRCULATION

This has been described in detail at an earlier period.

### THE ALLANTOIC CIRCULATION

We have already spoken of paired vessels extending through each segment of the embryo which arise from the aorta at about the level of the allantoic stalk. One pair of these segmental vessels increases in size as the allantois grows, and is distributed over the allantois in a rich plexus. As the allantois lies close under the shell, there is thus afforded a large area where gases can easily be exchanged and oxygenation be brought about. After such oxygenation and the extrusion of the carbon dioxide, the allantoic blood is gathered by the allantoic veins, and carried back to the heart.

The excretory ducts later develop in the embryo and then empty into the allantoic stalk close to its cloacal end. It is at this time that the allantois begins to function as a receptacle for solid waste matter, which, after the fluid parts have been evaporated, retains this waste-matter until it is thrown off at the birth of the animal.

The right and left allantoic veins run cephalad in the lateral body-walls of the chick, and enter the sinus venosus, one on each side of the omphalomesenteric vein. These two allantoic veins will shortly fuse and form a single **umbilical vein** (Fig. 308).

The yolk-sac is regarded as a diverticulum of the intestine, and the allantois as a diverticulum of the urinary bladder, which itself is an out-growth of the alimentary tract.

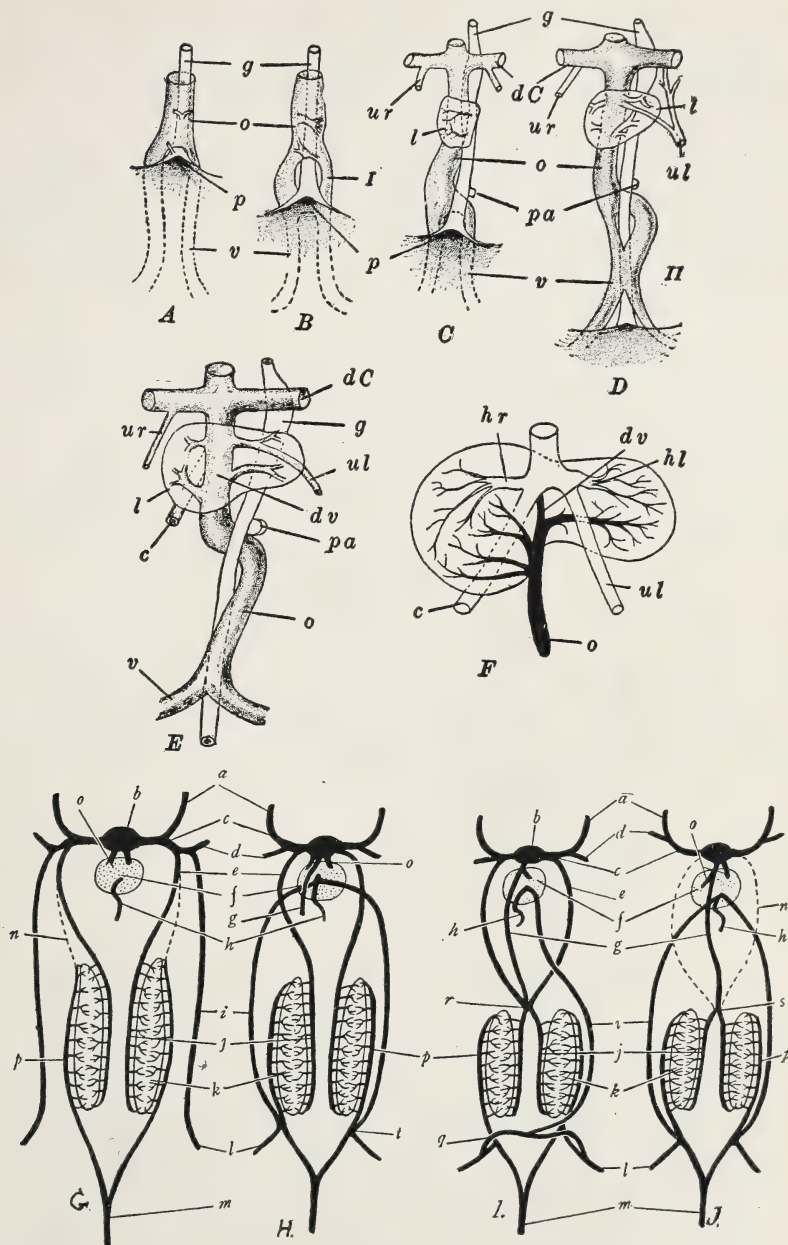


Fig. 308.

A to F, diagrams illustrating the formation of the omphalomesenteric and umbilical veins, in the chick. A. At about fifty-eight hours. B. At about sixty-five hours. Veins joined dorsal to the gut. C. At about seventy-five hours. Veins again separate. D. At about eighty hours. Secondary union of veins around the gut. E. At about one hundred hours. Definite arrangement of the vessels. F. Relationship of liver vessels. *c*. Vena cava posterior (inferior); *dC*, ductus

These outgrowths carry their blood vessels with them. Therefore, the omphalomesenteric artery and the vitelline veins (these latter are diverticula of the omphalomesenteric veins) extend out over the yolk, constantly increasing as to both absolute numbers and as to branches, as the yolk-sac spreads over the yolk.

The allantoic arteries are also called umbilical arteries. They are what will later be known as **hypogastric arteries**. In birds and reptiles five vessels, three arteries (one omphalomesenteric and two allantoic), and two veins (one vitelline, really omphalomesenteric, and one allantoic), connect the embryo freely through the umbilical stalk (Figs. 284, 297, 308).

In mammals, where there is little or no yolk, the yolk-sac is reduced or absent entirely and the omphalomesenteric and vitelline vessels disappear very early, so that the umbilical cord, or stalk, contains only the two allantoic arteries and one allantoic vein.

In the dogfish and all elasmobranchs, where there is a large yolk-sac but no allantois, the vitelline circulation alone is found, the allantoic not being present.

### THE INTRA-EMBRYONIC CIRCULATION

The large vessels communicating with the heart are the first ones to appear in the chick embryo. At thirty-three hours the ventral aorta extends headward, bifurcating ventral to the pharynx to form a single pair of aortic arches. This pair of arches passes dorsad around the pharynx and then runs tailward on the dorsal wall of the gut as the paired dorsal aortae (Fig. 277).

On the second day, as the visceral arches and clefts appear, this original pair of aortic arches comes to lie in the mandibular arch. In each of the visceral arches posterior to the mandibular, new aortic arches are formed, which connect the ventral aortae with the dorsal aortae.

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Cuvieri; *dv*, ductus venosus; *g*, gut; *hl*, left hepatic vein; *hr*, right hepatic vein; *l*, liver; *o*, omphalo-mesenteric vein; *p*, anterior intestinal portal; *pa*, rudiment of pancreas; *ul*, left umbilical vein; *ur*, right umbilical vein; *v*, vitelline vein; *I*, *II*, primary and secondary venous rings around the gut. (After Hochstetter.) *G* to *J*, Diagrams to show the origin of the postcaval vein and the changes in the abdominal vein in amphibians and reptiles. *G*, elasmobranch stage. The lateral abdominal veins *i* enter the common cardinal veins *c* and are not connected with the renal portal veins *p*. *H*, the lateral abdominals *i* have joined the renal portals at *i* posteriorly, and anteriorly pass into the liver *f*, where they unite with the hepatic portal vein *h*; a new vein, the postcaval vein *g*, is seen growing caudad from the liver *f*, where it arises from the hepatic veins *o*. *I*, condition in the adults of urodele amphibians; the postcaval vein *g*, has reached and fused with the posterior cardinals *e* and the subcardinals *j* at the point *r*; the two lateral abdominal veins have united to form the ventral abdominal vein *i* which empties into the hepatic portal *h*. *J*, condition in adult reptiles; the anterior portions of the posterior cardinal veins *n* are obliterated, leaving the postcaval vein *g* as the sole drainage for the subcardinals *j* and the kidneys *k*; the two lateral abdominal veins remain separate as in elasmobranchs. *a*, anterior cardinal vein; *b*, sinus venosus; *c*, common cardinal vein; *d*, subclavian vein; *e*, posterior cardinal vein; *f*, liver; *g*, postcaval vein; *h*, hepatic portal vein; *i*, lateral (or in *I*, ventral) abdominal vein; *j*, subcardinal vein; *k*, kidney; *l*, iliac or femoral vein; *m*, caudal vein; *n*, obliterated part of the posterior cardinals; *o*, hepatic veins; *p*, renal portal veins; *q*, pelvic veins; *r*, union of postcaval, posterior cardinals, the subcardinals; *s*, union of postcaval and subcardinals; *t*, union of abdominal vein with the renal portal system. (From Hyman's "A Laboratory Manual for Comparative Vertebrate Anatomy," by permission of The Chicago University Press.)

At fifty-five hours we saw there were three pairs of these aortic arches with a fourth pair just beginning to form. It is at about this period also that there is an extension headward from the dorsal aortic roots. These extensions form the **internal carotid arteries** which supply the brain.

The **external carotid arteries** arise later from the ventral aortic roots. They also grow cephalad as do the internal carotid arteries, but, unlike the internal carotids, the external carotids **supply the face**.

By the end of the fourth day two more pairs of aortic arches appear

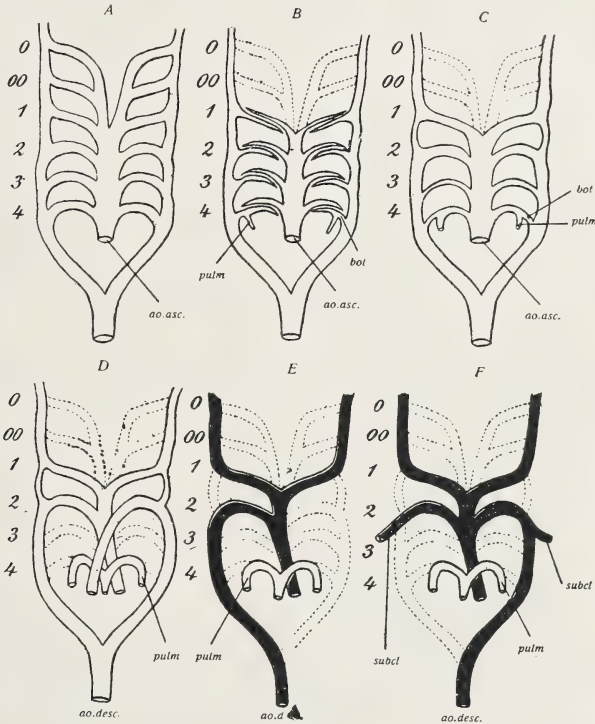


Fig. 309.

Schematic diagrams illustrating the changes which take place in the aortic arches. *A*, embryonic; prototype; *B*, Fishes; *C*, Urodeles; *D*, Lizard; *E*, Birds; *F*, Mammals.

The dotted lines show the portions which have become obliterated in the adult forms of the animals mentioned. *ao.asc.*, ascending aorta which branches into the following aortic arches: 0,00, 1, 2, 3, 4; *ao.desc.*, descending aorta; *bot*, duct of Botallus; *pulm*, pulmonary artery; *subcl*, subclavian artery; 0,00, 1, 2, 3, and 4, the six aortic arches. (After Boas.)

posterior to those already present. The fifth pair of aortic arches is very small and disappears in a short time.

The first and second arches have become smaller and also finally disappear. Probably most often the entire first arch has disappeared by this time and sometimes the second has also gone.

Consequently, there are present only the **third, fourth, and sixth**

pairs. While these arches do not remain intact permanently, though parts of them do, it is from these three pairs that the main blood vessels arise.

In reptiles, birds, and mammals, all the main vessels of the adult connecting the heart with the dorsal aorta are derived from the **fourth pair** of embryonic aortic arches.

It is important to remember this, as our studies in comparative anatomy will consist of the study of an **amphibian, a dogfish, a turtle, and a cat or rabbit**, and the student will be required to show similarities and differences of this nature in the different groups.

In reptiles the aortic arches remain in pairs (Fig. 309), but in birds **the left arch degenerates**, while in mammals it is **the right arch which degenerates**. The dorsal aortae, which began as paired vessels, now fuse close to the sinus venosus. The portion extending cephalad is fused for a very short distance, though never involving the region of the aortic arches.

Quite early in development there are segmental vessels arising from the aorta which extend into the dorsal body-wall. The pair at a level with the anterior appendage-buds enlarge and extend into the wing-buds as the **subclavian arteries**.

We have already mentioned the pair opposite the allantoic stalk which has enlarged to become the **allantoic arteries**.

The **external iliac arteries** which supply the posterior appendage-buds arise as branches from the allantoic arteries close to the origin of the aorta.

At four days, the chick embryo still has the omphalomesenteric arteries as its main visceral supply. It will be remembered that these arteries are paired originally. But as the embryo (which must be considered as having its ventral portion open and thus lying extended over the yolk of the egg), comes to have its ventral walls meet and grow together, the omphalomesenteric arteries, like the heart and other paired structures which later become fused to form a single vessel or organ, are brought together and fused, thus forming a single vessel which comes to lie in the mesentery and runs from the aorta to the yolk-stalk.

The proximal portion of the omphalomesenteric artery persists as the **superior mesenteric** of the adult, after the atrophy of the yolk-sac.

The **inferior mesenteric artery** and the **coeliac artery** arise from the aorta independently at a later stage.

The **cardinal veins** are the main **afferent systems** of the early embryo. They form on the second day as paired vessels on each side of the midline and extend both headward and tailward. The anterior and posterior cardinal veins on the same side come together to form the **duct of Cuvier**, which duct runs ventrally and enters the **sinus venosus**. On the fourth day there is practically no change in the cardinal veins.

Later, the proximal portions of the anterior cardinal veins become

connected by a new **transverse vessel** which forms and enters into the venous atrium of the heart, while the distal portions remain as the **jugular veins** of the head region.

The **posterior cardinal veins** (Figs. 301, 308) lie in the angle between the somites and the lateral mesoderm. It is of importance to locate these vessels and understand their position, as the excretory system develops in close relationship to them later, and their relation to the excretory system cannot be understood unless their developmental process is closely followed at this stage.

The mesonephroi develop **from the intermediate mesoderm** so that the posterior cardinal veins lie just dorsal to them throughout their length (Fig. 301).

In fact, the posterior cardinal veins are the principal afferent vessels of young embryos. However, in the adult these posterior cardinal veins will be replaced by the large **vena cava**.

With the foregoing in mind as a sort of general view of what has taken place and what will take place in the main blood vessels, we may enter into a little more detail.

## THE HEART

The heart began as a paired structure. When the ventral walls of the embryo came together, the two portions of the heart also came together to form a single tube in the midline of the body, close to the ventral portion.

After this fusion the heart is nearly straight and double-walled. The endothelial lining of the heart has the same structure and is continuous with the entering and outgoing blood-vessels.

There is a thickened layer over the heart, called the **epimyocardium**, which later separates into a thickened muscular layer, the **myocardium**, and a thin non-muscular covering called the **epicardium**.

As the paired tubes have come together to form the single heart, the splanchnic mesoderm from each side of the body has also come together to form the dorsal and ventral **mesocardia** (Fig. 275).

The ventral mesocardium disappears almost immediately after its formation, but the dorsal mesocardium continues suspending the heart for some little time, also disappearing ultimately, except at the more caudal portion of the heart.

The heart, now lying in the **pericardial** cavity, is attached at both ends and grows much more rapidly than the surrounding body, so that it begins to fold upon itself. The bending of the organ must be carefully studied, or later work upon the heart will have little meaning. (Figs. 274, 276, 279, 280, 283, 287.)

It will be noted that the cephalic end of the heart is attached just where the aortae leave it, while the caudal end of the heart is attached where the omphalomesenteric veins and the dorsal mesocardium meet.

It will also be noticed that the caudal or **ventricular** end grows toward the right.

The physical restriction placed upon the growing heart by the dorsal bending of the entire embryo, and the pushing in of the yolk dorsally, plus the fact that the entire embryo (by torsion) comes to lie upon its left side, accounts for the particular shape and direction of the heart's bending.

As the U-shaped bend continues to grow, the closed portion of the U is forced caudad and twisted upon itself to form a loop. This forces the **atrial** (venous region) portion slightly to the left (that is, toward the yolk) and the conus arteriosus is thrown across the atrial region by being bent to the right (or away from the yolk), and then caudad. The closed portion of the loop is the **ventricular region**. By this twisting process the original cephalo-caudal relations of the atrial and ventricular regions have become reversed, the atrial region now lying cephalad to the ventricle.

Not only has the position of the two regions become reversed, but a constriction is formed which divides atrium from ventricle (Fig. 283). The constriction itself forms the **atrio-ventricular canal**.

It is on the fourth day that the bulbus arteriosus, which lies across the atrium, presses down its ventral surface, thus beginning to indicate right and left divisions of the atrium. These divisions become complete later.

The ventricle has an indication of a right and left division also at this same time, caused by a longitudinal groove which appears on its surface.

The bulbus later divides to form the **root of the aorta** and the **pulmonary artery**.

Though the heart began its formation at the level of the hind-brain, it has come to lie now on a level with the anterior appendage-buds. The ventricular portion is the more unattached and so extends the more caudad.

Histologically, the endocardium of a four-day chick is still a single layer of cells, while the myocardium can be distinguished from the outer epicardium. The myocardium is composed of elongated cells which show some resemblance to the muscle cells they are to form. They are arranged in bundles extending toward the lumen. These bundles will become the **trabeculae carneae** of the adult heart.

The cells of the epimyocardium are becoming flattened to form the true epicardium, while loosely placed mesenchymal cells lie in the region between endocardium and myocardium near the atrio-ventricular canal. These mesenchymal cells will take part at a later period in forming the various septa which are to divide the heart into chambers as well as in forming the connective tissue frame-work of the valves.

The ventricular septum is completed at about the sixth day, its

anterior edge fusing with the posterior edge of the septum which divides the truncus arteriosus into right and left halves.

The anterior edge of the septum of the truncus arises between the fourth and fifth aortic arches in a manner which causes the blood coming from the left side of the truncus (that is, from the left ventricle) to pass through the third and fourth aortic arches, while the blood from the right ventricle passes into the fifth aortic arch.

About the seventh day the right and left parts of the truncus separate completely from each other. The right branch remains connected with the fifth aortic arch as the pulmonary trunk, and the left is connected with the third and fourth arches as the systemic trunk.

The ventral ends of the third arches become the subclavian arteries, carrying blood to the anterior appendages, while the dorsal communication between third and fourth arches disappears.

This means that the blood now passes from the left side of the heart through the third arch to the anterior appendages, and through the fourth arch to the dorsal aorta.

About the fifth day, the fourth pair of arches are the larger of any arches remaining, the left one, however, becoming smaller and smaller in size until it disappears almost entirely. The right fourth aortic arch grows larger and larger to form the **systemic arch** of the adult chick.

In mammals it is the right arch which disappears while the left alone persists as the systemic arch (Fig. 309).

Early on the third day, the **pulmonary arteries** form in the walls of the lungs and extend toward the fifth arch with which they connect at the ventral ends of these arches. The dorsal end of the fifth arch, between the point of union of the pulmonary artery and the dorsal aorta, is called the **duct of Botallus** (Fig. 309). This ductus Botalli offers the blood from the right side of the heart a passage into the dorsal aorta so that little passes through the capillaries. The duct, however, shrivels up at the time of hatching, and becomes entirely closed so that all the blood from the right side of the heart must pass into the pulmonary circulation. It is at this time that the lower portion of the aortic arch becomes the pulmonary artery.

## THE VEINS

The anterior and posterior cardinal veins unite with each other on a side to form the duct of Cuvier and then enter into the **meatus venosus**. These anterior and posterior cardinals bring back the blood to the heart from practically all parts of the body except the digestive organs.

The anterior cardinals persist as the **jugular veins** to which the **pectoral veins** from the anterior appendages soon become joined. From the head and neck the **vertebral veins** also join the jugulars.

The posterior cardinals remain large as long as the Wolffian body

is functional, but as the permanent kidneys develop, these veins become smaller and smaller and ultimately disappear.

The ducts of Cuvier persist in the adult chick as the **anterior venae cavae**.

The **posterior** or **inferior vena cava** develops from the meatus venosus, which was formed by the union of the two omphalomesenteric veins. To understand the evolving process by which the posterior vena cava comes into existence, it is necessary to follow carefully the development of the surrounding organs.

The liver forms as a diverticulum from the digestive tract. This diverticulum then grows around the meatus venosus until it completely surrounds the meatus. Blood-vessels form in the liver, extending toward the meatus venosus, into which they open by the fifth day.

At the posterior edge of the liver, there are a number of **afferent** hepatic vessels coming from the meatus venosus through which some of the blood coming to the heart from the vascular area may enter the capillaries formed in the liver substance.

At the anterior edge of the liver, where the meatus venosus might be said to be leaving the liver, there is a collection of **efferent hepatic** vessels whose distal ends are in direct connection with the capillaries of the afferent hepatic vessels.

The blood passing through the liver has two courses it may take. Most of it passes through the large meatus venosus into the heart, but some of it passes through the afferent hepatic vessels into the liver substance where it is collected by the efferent hepatic vessels and is carried to the meatus venosus.

That part of the meatus venosus lying between the afferent and efferent hepatic vessels, is often called the **ductus venosus**.

The two allantoic veins already described unite on entering the body to form a single vein emptying into the left (persistent) omphalomesenteric vein. It is well to remember that as the yolk-sac decreases in size, the allantois increases, and so, too, the relative size of omphalomesenteric veins and allantoic veins changes; the omphalomesenteric becomes smaller and the allantoic becomes larger, so that it almost seems as though the omphalomesenteric were a branch of the allantoic. Both of these veins disappear at the time of hatching.

The superior mesenteric artery was formed by the closure of the ventral body-wall so as to bring the paired omphalomesenteric veins together, to form a single vessel running from the aorta to the yolk-stalk. As the yolk-sac atrophies, the proximal portion of the omphalomesenteric artery becomes the superior mesenteric artery.

The **mesenteric vein** is formed by a union of the veins from the walls of the hinder part of the digestive tract, which there form a single vein. This vein is at first quite small, and empties into the omphalomesenteric vein just before the latter enters the liver. The point of entry may be

said to be the beginning of where the omphalomesenteric vein becomes the meatus venosus.

It will be noted, therefore, that the blood which goes to the liver comes from three sources:

(1) Through the omphalomesenteric vein, from the yolk-sac. This blood is rich in food material and has been oxidized in the vascular area.

(2) Through the allantoic vein from the allantois. This blood is very rich in oxygen.

(3) Through the mesenteric vein from the digestive tract of the embryo. This blood is venous in character.

The **mesenteric vein** increases in size with the growth of the embryo, and after the omphalomesenteric and allantoic veins disappear at the time of hatching, it persists as the **hepatic portal vein** of the adult chick. This large vessel brings blood back from the hinder parts of the digestive canal to the liver.

On the fourth day, the posterior, or inferior, vena cava proper arises. It forms between the posterior ends of the Wolffian bodies, and runs forward in the midline, ventral to the aorta. It joins the meatus venosus anteriorly between the heart and the anterior edge of the liver, and posteriorly it connects with the permanent kidneys as soon as these are formed. It also connects posteriorly with the hind limbs and the caudal region.

The posterior vena cava is at first quite small, but as more and more blood is sent from the developing metanephroi and the caudal region, it becomes even larger than the meatus venosus of which it was originally but a branch.

Just before the vena cava becomes larger than the meatus venosus, the efferent hepatic vessels have shifted their position so that they now enter directly into the vena cava instead of the meatus as formerly. In fact, before the time of hatching the entire portion of the meatus venosus lying between the heart and liver becomes obliterated, so that all blood flowing into the posterior end of the liver through the portal vein, passes into the posterior vena cava through the hepatic vein (Fig. 308, I, J).

The relative changes in the size of blood vessels must be clearly understood and followed, or the circulatory system of the embryo, and consequently, also the circulation of the adult will be hopelessly confused.

It is well at this point to obtain an idea of the embryonic circulation of a little later time than that of the fourth day which we have been discussing.

By the beginning of the sixth day, the septa, which have already been mentioned, have divided both auricles and ventricles into right and left halves (Fig. 283). However, neither of these septa are complete. The septum that separates the two parts of the auricle develops perforations, and in the human heart these perforations form an oval-shaped opening

called the **foramen ovale**, which may, in the abnormal cases, remain open and thus cause a constant intermingling of venous and arterial blood. Usually, such persons do not live long, although there are notable exceptions. This inter-auricular foramen closes at the time of hatching, so that the blood from the right auricle can be sent to the lungs for aeration as soon as these organs become functional at birth.

The septa are sufficiently developed so that we may speak of four divisions or cavities in the heart. This makes a double circulation possible, namely, the systemic and the pulmonary (up to the time of hatching, the allantoic circulation takes the place of the pulmonary).

By this time, then, the heart is fully formed. The sinus venosus has been absorbed into the right auricle, of which it forms a part. The open foramina allow blood to pass back and forth between the auricles. The ventricular septum is more complete. The truncus arteriosus is divided into two separate vessels: the pulmonary trunk arises from the right ventricle, and the systemic trunk arises from the left ventricle.

The aortic arches which are still present are the third, fourth, and fifth, and small portions of the first and second.

The systemic trunk from the left ventricle leads to the third and fourth pairs of aortic arches, from which the head and fore-limbs are supplied.

The pulmonary trunk, arising from the right ventricle, leads to the fifth pair of aortic arches, which are directly continuous with the dorsal aorta. It is from these that the small pulmonary arteries arise.

It will be remembered that, as the lungs are not yet functional, there is little use for these vessels until later. An omphalomesenteric artery carries blood to the yolk-sac, and a large allantoic artery passes from the aorta to the allantois.

The venous system consists of the right and left anterior venae cavae, and the posterior vena cava. The former drain the head and fore-limbs, and the latter the posterior portions of the body, the limbs, and the kidneys.

Before reaching the heart, the posterior vena cava is joined by the ductus venosus (through which blood is returned from the yolk-sac, allantois, and embryonic alimentary canal) by the omphalomesenteric, allantoic, and mesenteric veins respectively.

All three venae cavae open into the right auricle of the heart, but due to the position and direction of the opening, and to a valve, the blood from the posterior vena cava is directed through the foramen ovale into the left auricle, while the blood from the right and left venae cavae (anterior) remains in the right auricle.

As the auricles now contract, the blood which has come from the posterior vena cava is forced into the left ventricle and passes out through the systemic trunk through the third and fourth pairs of aortic arches to the head and fore-limbs, while the blood from the anterior

venae cavae passes out through the right ventricle through the pulmonary trunk and thus through the fifth aortic arches into the dorsal aorta, from where the blood goes to the body and hind-limbs of the embryo. A small portion, however, is carried out along the omphalomesenteric arteries to the yolk-sac and through the allantoic arteries to the allantois to take up nutriment and oxygen. In the early embryo, a much greater portion of this pulmonary circulation goes to yolk-sac and allantois.

It is assumed that the vastly greater proportion of blood supply to the anterior region, as contrasted with the smaller quantity to the posterior portions, accounts for the greater and more rapid development of the head region, which, it will be remembered, is the first part of the chick to develop.

The disproportionate development of the head may be realized when it is known that the human child at birth has a head about one-fourth the length of its entire body, while in adults the head extends to only one-seventh of the body's length.

At about the time of hatching, the ductus Botalli (which it will be remembered is that portion of the fifth aortic arch lying between the dorsal aorta and the point of origin of the vessel that runs to the lung)—(Fig. 309)—closes up entirely, so that the blood from the right ventricle must pass through the pulmonary veins back to the left auricle.

The lungs now become functional and the true pulmonary circulation is established. The allantoic circulation, which is no longer needed, ceases, while the allantoic arteries and veins disappear, as do also the omphalomesenteric arteries and veins when the yolk-sac has finished its work, and the hatched chick can take in its own food.

It is at this time also that the entire supply of blood, which goes to the liver, passes through the mesenteric vein, which is now called the **hepatic portal vein**. The ductus venosus has closed, and so all blood brought to the liver must pass through the hepatic capillaries before reaching the heart.

The foramen ovale does not close immediately after hatching, but does so in a few days. As soon as it does, all blood returned to the heart by the three venae cavae is emptied into the right auricle from which it is then forced into the right ventricle, thence through the pulmonary artery to the lungs, and back through the pulmonary veins to the left auricle, from which it is forced into the left ventricle, and finally through the systemic trunk. Such an entire separation of venous and arterial blood is called a **double circulation**.

## CHAPTER X

### THE COELOM AND THE MESENTERIES

**I**N OUR account of the earthworm (Vol. I), the student was introduced to all higher forms of animals possessing a coelom or body-cavity. The chapter on the earthworm should be reviewed at this point.

Then, too, in the early part of our work on chick embryology, we have seen how the mesoderm divided into splanchnopleure or somatopleure, and how the organs growing out from their respective beginnings pushed a layer of one of these coverings before them. And we have also seen how the chick embryo is quite similar to an animal which has had a ventral incision made along the midline and then had these two halves stretched over a yolk-sphere so that its organs or portions of organs, which developed from two primordia or beginnings, later came together when the fusion of the ventral body walls produced a single organ of the two separated halves.

In adult birds and mammals, the coelom, or body-cavity, consists of three regions, known as **pericardial**, **pleural**, and **peritoneal**. The pleural region is paired, each half containing **one lung**. The other two chambers are unpaired. The pericardial region contains the **heart**, and the peritoneal region contains all the **abdominal viscera**.

As the coelom arises by a splitting of the mesoderm, and the two halves of the chick are spread out over the yolk, the coelom is naturally a paired cavity, only becoming a single cavity when the ventral body walls of the embryo come together, and the ventral mesentery then disappears.

There are no segmental pouches in the chick coelom as there are in some of the lower vertebrates, though it cannot be said that this is unlike the lower forms; for, by the time the coelom appears in the chick, the pouches would already be broken through any way, and have become connected.

As the mesoderm splits and the splanchnopleure and somatopleure extend out over nearly the entire yolk-sac, it is to be understood that much of this split mesoderm is **extra-embryonic**. This has already been described in an earlier chapter.

Here we are concerned with the **embryonic coelom**.

The portion of the embryonic coelom which gives rise to the three body-cavities mentioned above is marked off by a series of folds which separate the body of the embryo from the yolk. With the closure of the ventral body walls, the embryonic coelom becomes completely separated from the extra-embryonic though in the yolk-stalk region it remains open much longer than in other portions (Fig. 281, C to G).

It is this same closure of the ventral body walls which also brings the two portions of the gut together ventrally. This causes the newly-closed gut to lie between the two layers of splanchnic mesoderm, while the body-spaces on each side form a right and left coelomic chamber. In fact, there are **double layers** of mesoderm which enclose and support the gut. These double layered supports are called **mesenteries**. The dorsal mesentery remains as a continuous support—at least the greater portion of it does—but the ventral mesentery soon disappears, causing the right and left coelomic cavities to become confluent.

In the liver region, however, the ventral mesentery does not disappear (Fig. 293). The liver arose by a ventral outgrowth of the gut and extended into the ventral mesentery. As the liver grows ventrally from the digestive tract there is a portion of the ventral mesentery lying dorsal to the liver, that is, between the liver and the gut. This persists as the **gastro-hepatic omentum** while the portion ventral to the liver is called the **ventral ligament** or the **falciform ligament**.

The dorsal mesentery persists, as stated, but has different names in different parts, i. e., **mesocolon**, where it supports the colon, **mesogaster**, where it supports the stomach, etc.

Septa grow out from the body wall to divide the body-cavity into the pericardial, pleural, and peritoneal chambers mentioned above.

## CHAPTER XI

### DEVELOPMENT OF THE FIFTH DAY

ON THIS day the head and tail of the embryo have nearly come together by the great curving of the chick. The yolk is completely covered by the blastoderm while nearly two-thirds of the blastoderm is vascular area.

#### THE LIMBS

It is during this day that the limb-buds increase considerably in size, and are marked off into a proximal rounded portion and an expanded distal region. It is in the expanded distal region that the digits can be seen to form in cartilage. The rounded proximal portion is slightly bent at the points where elbow and knee joints will be formed.

The elbow and knee-angles at first are directed almost straight out from the body, but on about the eighth day both fore and hind-limbs rotate until the elbow-joint points caudad, while the knee-joint points cephalad.

By the end of the tenth day, both pairs of appendages have their definite outlines, though feathers and nails are not yet formed.

Although the structures which are to become bones are first outlined in cartilage, they later become **ossified**. There are three well-formed digits in the expanded distal portion of the fore-limb at this time with a possible fourth in a rudimentary condition, while in the expanded distal portion of the hind-limb there are also three well-defined digits with two in a rudimentary condition.

The development of the bony vertebrae has already been discussed. Here it is well to state that the ribs develop as cartilaginous bars in the body wall of the chick. The ventral ends of these fuse ventrally, and after fusion, a portion of each of the fused ends separates from the remaining ribs from which they formed. It is this portion which has separated that becomes the **sternum**.

#### THE DEVELOPMENT OF THE SKULL

The skull is divided into two regions: (1) The **skull proper**, and (2) the **visceral skull**. This latter is that portion of the skull which has developed from the visceral arches.

#### THE SKULL PROPER

The notochord forms a sort of central portion around which the vertebrae form. The anterior end of the notochord serves a sort of similar function in the head region.

On each side of the notochord, a sheet of cartilage develops. These two sheets are known as **parachordal plates** (Fig. 310). They form a

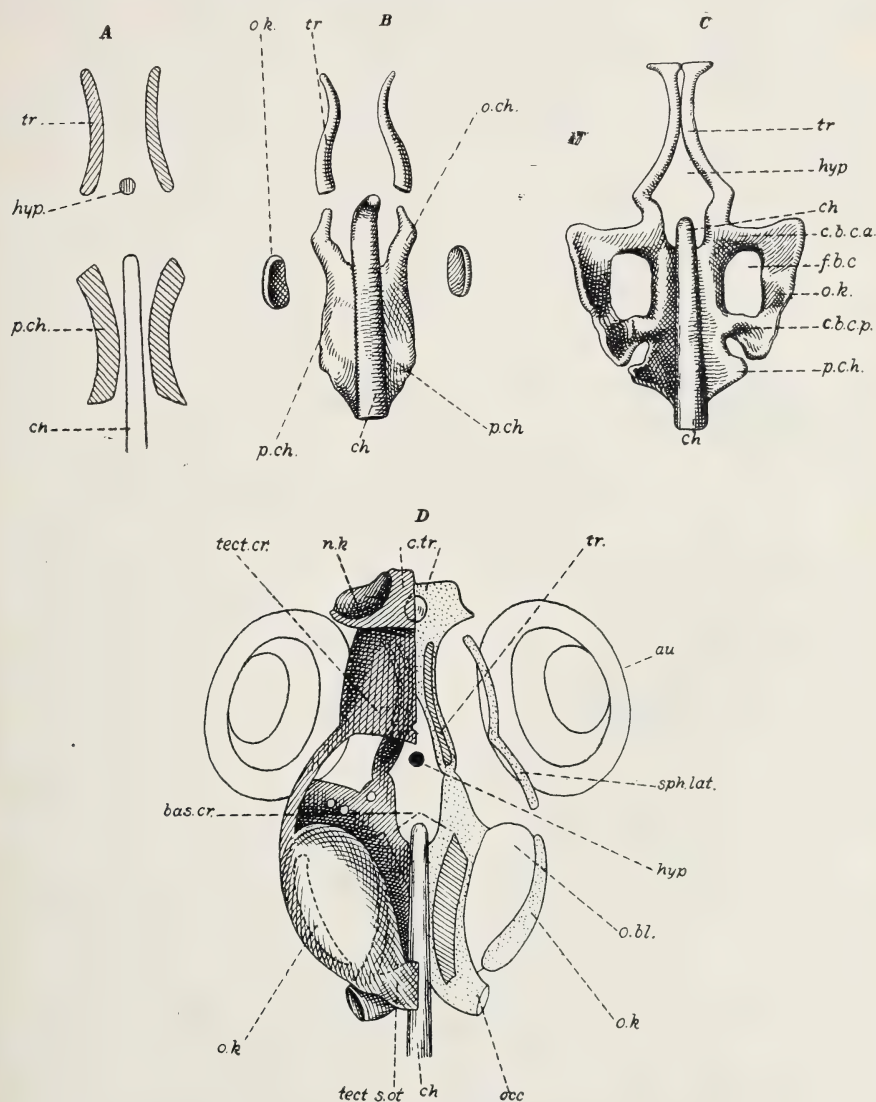


Fig. 310.

Diagrams of skull formation in Salmon. *A*, first anlage of cranium. *B*, *C*, *D*, successive stages in cranial development. Left half of *D* is an advance in development of right half. *au*, eye; *bas.cr.*, base of cranium; *c.b.c.a.*, *c.b.c.p.*, anterior and posterior basicapsular commissure (ascending process of palatoquadrate cartilage); *ch*, notochord; *c.tr.*, trabecular cornu; *hyp*, opening in which hypophysis develops; *n.k.*, nasal capsule; *o.bl.*, and *f.b.c.*, fenestra basicapsularis; *o.k.*, ear capsule; *occ*, occipital region; *p.ch.*, parachordal plates; *sph.lat.*, lateral sphenoid; *tect.cr.*, roof of cranium; *tect.s.ot.*, cartilaginous arch between otic capsules representing the cartilaginous roof of higher vertebrates (tectum synoticum); *tr.*, cranial trabeculae. (*A*, *D*, after Waskoboynikow; *B*, *C*, from Gaupp after Stöhr's model.)

floor for the mid and hind-brains. These plates then fuse both dorsally and ventrally around the notochord, and consequently enclose it. The fused plate is then known as the **basilar plate** and forms the floor of the hinder portion of the skull.

The **auditory capsules** which enclose the auditory organs form and fuse to the sides of the basilar plate. It is from growths of the basilar plate and the auditory capsules that the floor and occipital portions of the skull are formed.

The anterior portion of the skull is formed from two slender rods lying cephalad to the notochord but which are in connection with the parachordal plates. These rods are known as **trabeculae cranii**.

The pituitary body lies between these trabeculae cranii, so that in fusing as they now do to form the **ethmoid plate**, the pituitary body comes to lie in the position where it will be found when we study the structure in Comparative Anatomy.

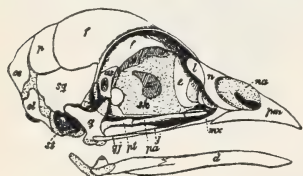


Fig. 311.

Profile view of 2-day chick-skull. *as*, alisphenoid; *d*, dentary; *e*, ethmoid; *f*, frontal; *l*, prefrontal; *mx*, maxillary; *n*, nasal; *ol*, lateral occipital; *os*, superior occipital; *pa*, palatine; *pm*, premaxillary; *pt*, pterygoid; *q*, quadrate; *qj*, quadrato-jugal; *na*, cartilaginous wall of nasal cavity; *sq*, squamosal; *st*, columella; *sk*, and *x*, cartilaginous portion of skull just becoming converted into bone. (Cartilage is stippled.) (After Boas.)

while the membranous bones were first cartilage, and then, by being placed where there was considerable stretching, they became quite thin membranes before they finally ossified.

The **membranous bones** form the roof of the skull, such, for example, as the parietals, frontals, etc.

## THE VISCERAL SKULL

It will be remembered that the first visceral arch was also called the mandibular arch, because it is from this arch that the mandible, or lower jaw, is formed,<sup>1</sup> and that the second visceral arch was known as the hyoid arch, because it is from this that the hyoid bone, or cartilage which supports the tongue, has developed. The parts of the skull which are thus developed from the visceral arches form the visceral skull.

## THE HEART

It is during the fifth day that the **interventricular septum** is almost completed, fusing with the posterior edge of the septum which now

<sup>1</sup>The bones of the upper jaw also form from the mandibular arch.

develops in the truncus arteriosus. This latter septum is formed between the fourth and fifth pairs of aortic arches and follows a sort of spiral course caudally to where it joins the interventricular septum. It is the position and shape of these septa which cause the blood to course into the different channels as described for the fourth day.

Two sets of **semilunar valves** have now formed between the two divisions of the truncus arteriosus and the two ventricles into which they open. The heart continues growing, but it is not until about the twelfth day that the **interauricular septum** has almost completely closed, leaving only the **foramen ovale** as a small opening between the two auricles. The foramen ovale develops a little fold of membrane which closes the opening entirely some days after hatching.

The ventricles now become thickened to a very considerable extent. The auricles likewise thicken but not to so great an extent as the ventricles. The ventricular thickenings on the inside of the heart form as an inward growth of ridges which are called **trabeculae carneae**. They are really separate muscle-bundles which help to open and close the valves.

On the sixth and seventh day the distinctly bird-like characteristics appear. Up to this time the beginner cannot tell the difference between a chick embryo and that of practically any other one of the higher vertebrates.

The nasal region now begins to lengthen and the fore-limbs will be seen to develop into wings.

The allantois has become very large and contains a considerable amount of fluid.

The omphalomesenteric arteries and veins now pass from the body of the embryo as single vessels. The yolk, though seemingly as large as before, is quite liquid in form.

The flexion of the body is less marked than before, while the head is not so large in proportion to the remainder of the body as formerly.

The cerebral hemispheres can be seen quite plainly, as well as the beginnings of the tongue-bud.

On the next three or four days the little sac-like regions in which the feathers develop make their appearance as protrusions from the surface, especially on the dorsal side of the chick, while a chalky patch at the tip of the nose marks the beginning of the horny beak. The yolk has become wrinkled and flabby.

After the eleventh day, the abdominal walls become firmer and the intestines are enclosed in the peritoneal cavity. The body is now complete except for the narrow stalks of the umbilicus and yolk-sac. The amniotic fluid tends to disappear, which makes the amnion less prominent.

By the thirteenth day the feathers are well distributed over the entire body although they do not break through their sacs until about

the nineteenth day. By this time they are approximately an inch in length.

On the thirteenth day the nails and scales appear on the toes, and by the sixteenth day nails, scales, and beak are firm and well developed. On this day also the cartilaginous skeleton completes its growth, and various **centers of ossification** make their appearance.

By the sixteenth day the white of the egg has disappeared and the mesoderm has divided completely into the splanchnopleure and somatopleure all the way around the yolk.

On the nineteenth day the remains of the yolk are drawn into the body cavity of the embryo.

The embryo begins its development originally by lying with its axis transverse to the long axis of the egg, but by the fourteenth day it turns so that its head is toward the air space at the larger end of the egg, and at about the twentieth day the chick's beak is pushed through the inner covering of the air space so that it can now begin using its lungs. It is at this time that the pulmonary circulation begins. The blood stops flowing into the umbilical vessels and the allantois consequently shrivels up and is left inside the shell as the chick pecks its way out.

## CHAPTER XII

### THE EMBRYOLOGY OF THE FROG

#### The General Embryology of the Tadpole as Compared with that of the Chick

**A**S IN our study of the Embryology of the chick, it is essential that the student again read the chapters on mitosis, fertilization, and the summary on Embryology, and then go over each system in the developing chick corresponding to the system he may be studying in the frog. Only in this way can the comparison of the developmental processes be understood.

After this has been done, the following groups of **Craniata** must be kept clearly in mind to make clear the various embryological relationships which must be referred to, not only in the study of Embryology, but also in Comparative Anatomy.

### CLASSIFICATION OF CHORDATA

(After Newman)

Sub-Phylum I. Cephalochordata (Adelochorda), (Fig. 312).

I.

II.

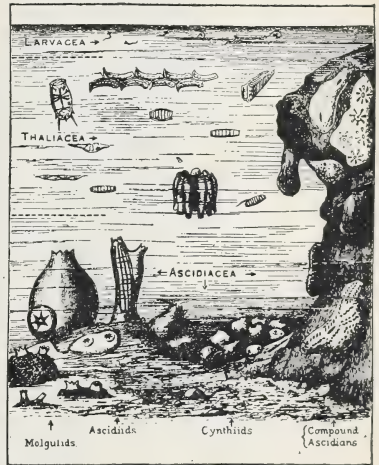
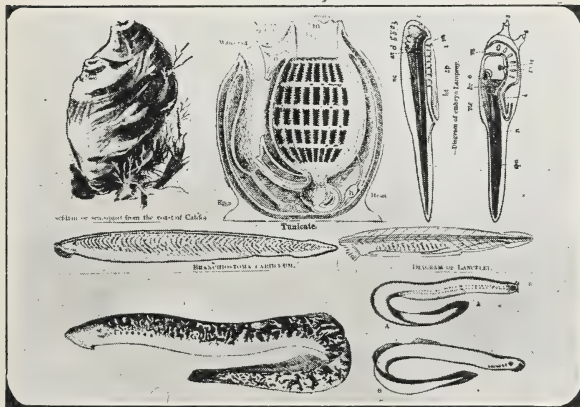


Fig. 312.

I. Examples of *Amphioxus* (*Branchiostoma* and *Lancelet*), *Tunicates* (First two upper figures), *Lamprey* (The large, lower, left-hand figure-adult; and the embryo lamprey, usually called *Ammocoetes*—2 upper right-hand figures), and the *Hagfish* (2 lower right-hand figures).

II. Sketch of chief kinds of *Urochordata* showing distribution in sea. Dotted lines on left indicate life-zones. The surface is called the pelagic zone. (From Herdman.)

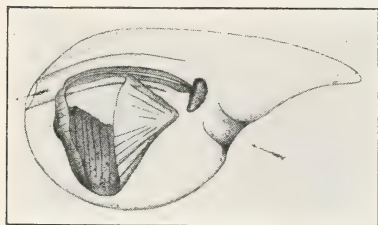
This includes but a single family of fish-like creatures, of which there are about twelve species. The type form is **Amphioxus** more correctly known as **Branchiostoma**.

## Sub-Phylum II. Urochordata (Figs. 312, 313).

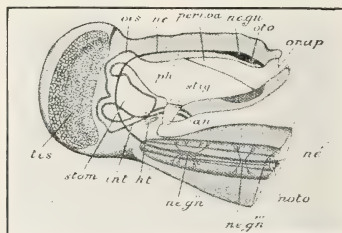
Order 1. **Larvacea (Appendicularia)**, free-swimming forms with permanent tail.

Order 2. **Ascidacea (Tunicates or Sea-Squirts)**, fixed forms without tail in the adult.

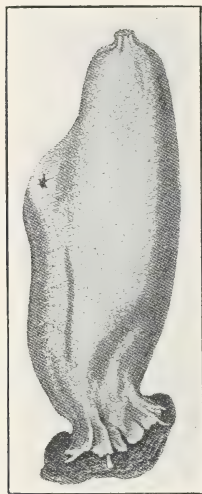
Order 3. **Thaliacea (Salpians)**, free-swimming forms without tail in the adult.



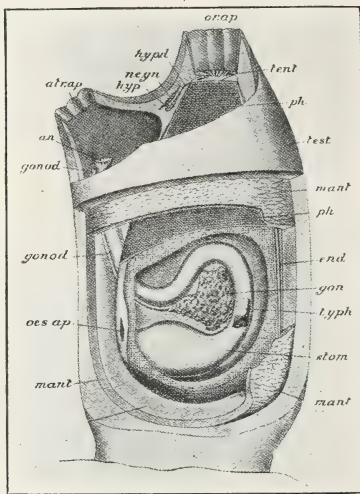
I.



II.



III



IV.

Fig. 313.

## UROCHORDATA.

I. *Oikopleura* in 'house'. The arrow shows course of current.

II. Diagram of *Appendicularia* from the right side. *an*, anus; *ht*, heart; *int*, intestine, *ne*, nerve; *ne'*, caudal portion of nerve; *ne.gn'*, principal nerve ganglion; *ne.gn''*, *ne.gn'''*, first two ganglia of tail nerve; *noto.*, notochord; *oes.*, oesophagus; *or.ap.*, oral aperture; *oto*, otocyst (statocyst); *peri.bd.*, peripharyngeal band; *ph.*, pharynx; *tes.*, testis; *stig.*, one of the stigmata; *stom.*, stomach. (After Herdman.)

III. and IV. *Ascidia*. Entire animal as seen from the right side and dissection from the same side. *an*, anus; *atr.ap.*, atrial aperture; *end*, endostyle; *gon*, gonad; *gonad*, gonoduct; *hyp*, neural gland; *hyp.d*, duct of neural gland; *mant*, mantle; *ne.gn.*, nerve-ganglion; *oes.ap.*, aperture of oesophagus; *or.ap.*, oral aperture; *ph*, pharynx; *stom*, stomach; *tent*, tentacles; *test*, testes. (After Herdman.)

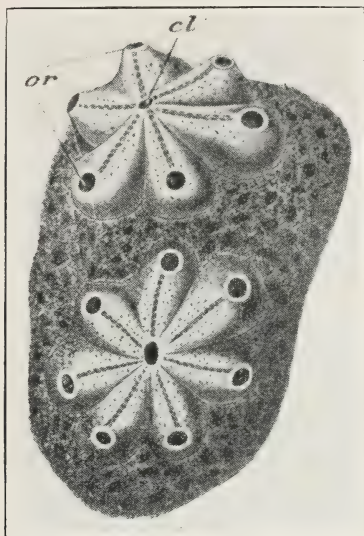
## Sub-Phylum III. Hemichordata (Fig. 314).

Order 1. **Enteropneusta**, including worm-like forms such as **Balanoglossus**.

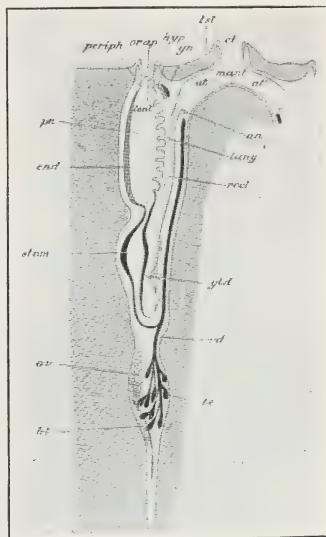
Order 2. **Petrobranchiata**, sessile, tube-dwelling forms—**Cephalodiscus** and **Rhabdopleura**.

Order 3. **Phrononidia**, tube forms—**Phoronis** (Fig. 199, Vol. I).

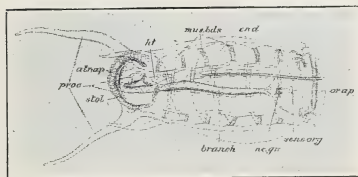
Sub-Phylum IV. **Vertebrata** (Craniata).



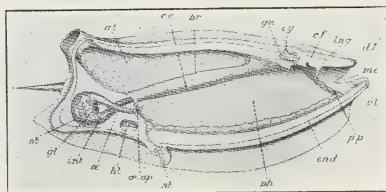
V.



VI.



VII



VIII.

Fig. 313.

V. *Botryllus violaceus*.

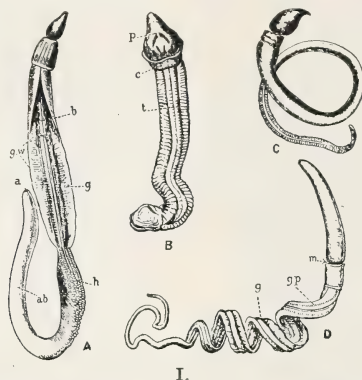
VI. *Composite Ascidian*. Diagram of an individual member of a colony of composite Ascidians. The zooids are in pairs and seen in vertical section. *an*, anus, *at*, atrium; *at'*, atrium of adjoining zooid; *cl*, cloaca common to both zooids; *end*, endostyle; *gld*, digestive gland; *gn*, nerve ganglion; *ht*, heart; *hyp*, neural gland; *lang*, languet; *mant*, mantle; *or.ap*, oral aperture; *ov*, ovary; *periph*, peripharyngeal band; *ph*, pharynx; *rect*, rectum; *stom*, stomach; *te*, testis; *tent*, tentacles; *tst*, test or common gelatinous mass in which individuals are imbedded; *v.d*, vas deferens (V, after Mile-Edwards; VI, after Herdman.)

VII. *Salpa democratica*, asexual form, ventral view, and VIII lateral view in section. *at*, atrial cavity; *atr.ap*, atrial aperture; *br*, branchia; *branch*, dorsal lamina; *c.c*, ciliated crests on edge of branchia; *c.f*, ciliated funnel; *d.l*, dorsal lip; *end*, endostyle; *ey*, eye; *gl*, digestive gland; *gn*, ganglion; *ht*, heart; *int*, intestine; *lng*, languet; *mo*, mouth; *mus.bds*, muscular bands; *me.gn*, nerve-ganglion; *æ*, oesophagus; *oe.ap*, and *or.ap*, apertures of oesophagus and mouth; *ph*, pharynx; *pp*, peripharyngeal band; *proc*, processes at posterior end; *sens.org*, sensory organ; *st*, and *stol*, stolon; *st*, on left, stomach; *v.l*, ventral lip. (VII, after Vogt and Jung, VIII, after Delage and Herouard.)

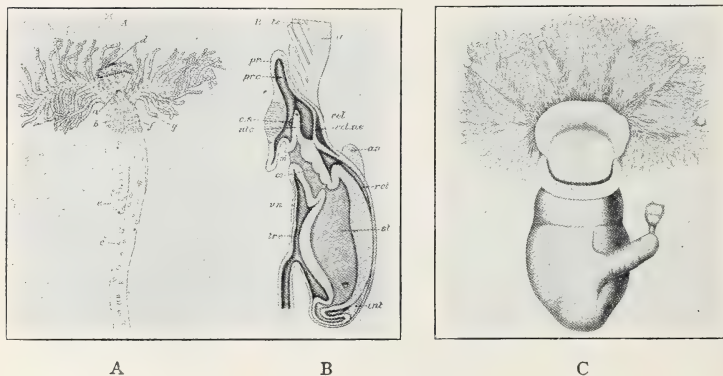
Order 1. **Cyclostomata** (round mouth eels), such as hagfish and Lampreys (Fig. 312).

Order 2. **Pisces** (true fish with jaws).

- Order 3. **Amphibia** (vertebrates with aquatic larvae, but usually air breathing in the adult condition), (Fig. 315).  
 Order 4. **Reptilia** (cold-blooded, air-breathing vertebrates).  
 Order 5. **Aves** (birds, feathered vertebrates).  
 Order 6. **Mammalia** (beasts or quadrupeds).



I.



A

B

C

II.

Fig. 314.

## HEMICHORDATA.

I. Various types of *Enteropneusta* which are relatives of *Balanoglossus*. *A*, *Balanoglossus clavigerus*; *B*, *Glandiceps hacksii*; *C*, *Schizocardium brasiliense*; *D*, *Dolichoglossus kowalevskii*; *a*, anus; *ab*, abdominal and caudal regions; *b*, branchial region; *c*, collar; *g*, genital region; *gp*, gill-pore or branchial cleft; *an*, genital wing; *h*, hepatic region; *m*, position of mouth; *p*, proboscis; *t*, trunk. (From Newman, *A*, *B*, *C*, after Spengel, *D*, Bateson.)

II. *A* and *B* *Rhabdopleura*, *C*, *Cephalodiscus dodecalophus*. *A* and *C*, entire animals. *B*, diagram of median longitudinal section of *A*. *A*, *a*, mouth; *b*, anus; *c*, stalk of zooid; *d*, proboscis; *e*, intestine; *f*, anterior region of trunk; *g*, one of the tentacles. (After Ray Lankester.) *B*, *a*, arm; *an*, anal prominence; *col*, collar; *col.n*, collar nerve; *c.s*, cardiac sac; *int*, intestine; *m*, mouth; *ntc*, notochord; *oe*, oesophagus; *pr*, proboscis; *pr.c*, proboscis-coelom; *rct*, rectum; *st*, stomach; *te*, tentacles; *tr.c*, trunk-coelom; *v.n*, ventral nerve. (*B*, after Schepotieff, *C*, after McIntosh.)

## EMBRYOLOGY OF THE FROG

The frog is usually considered a transitional form separating the lower from the higher craniata both embryologically and anatomically. And, although the craniates vary considerably among themselves, the frog has enough in common with all such variations to make it a norm,

or standard type, for constant and valid reference, both as to anatomy and development. The adoption of a standard makes an understanding possible of any special modifications one may find.

Then, so much work has been done in this field that a thorough understanding of the embryology of the frog is essential to anyone who wishes to do advanced work in the zoölogical sciences.

Just as there are various groups of birds with different hatching periods, so different species of frogs also vary as to the length of time the embryo requires before being able to emerge from the egg. But,

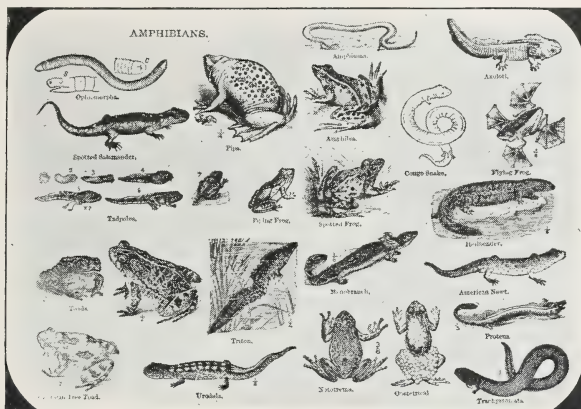


Fig. 315. Examples of tailed and tailless Amphibia.

unlike the birds, the frog passes through a process of **metamorphosis**, which simply means that even after the embryo's emergence from the egg, it does not have the adult form, but must pass through still further changes before becoming a full-fledged frog. In the frog the form which is assumed at the time of hatching and which later changes on arrival at adult life, is called the **tadpole** stage.

Temperature has much to do with both the rapidity with which a frog's egg develops, and with which the tadpole develops into an adult frog. This, however, is not unlike the hen's egg; for, it will be remembered that after the hen's egg was fertilized and the embryo had already begun to develop (before the egg has been laid), such an egg could be placed in a moderately cool place for many days, which would result in all development ceasing. If the egg is then placed under a hen or in an incubator, the embryo again begins to develop.

We shall arrange our study of the frog under two headings: **First**, the **true embryonic period**. This extends from the time the egg is fertilized through **blastulation** and **gastrulation**. During this time the **germ layers** as well as the larval and tadpole organs form. This period extends up to the time the tadpole emerges from the egg.

**Second**, the **larval period**, from the time of hatching to the time when the legs are formed, the tail is thrown off, and the animal has become a

full-fledged frog with all its various organs and the form which it is to retain throughout adult life.

To grasp fully that which follows, it is necessary to review the account of the reproductive organs in the chapter on the frog in Volume I of this work.

As the sperm from the male frog never enter the female body, the egg must be fertilized after it has been laid. This is quite different from fertilization in the hen. During the breeding season, as the eggs are squeezed from the female, the male passes over the eggs and deposits his sperm upon them. The fertilized eggs begin to divide almost immediately, and within approximately thirty-six hours the blastula stage has been reached. In about six days, when the embryo is five millimeters in length, there is already a twitching within the egg, showing that life is present, and within two weeks after fertilization the embryo wriggles its way out of the surrounding jelly and becomes a free-living **larva** or **tadpole**. This is the end of the true embryonic period.



Fig. 316.

A frog embryo at the stage of hatching. *an.*, Proctodæum; *au.c.*, slight swelling over the rudiment of the ear; *e.g.*, external gills on gill arches; *na.*, invagination to form nasal capsule; *o.c.*, slight swelling over the rudiment of eye; *s.*, sucker; *stm.*, stomodæum (invagination which will form the mouth. (After Borradaile.)

bottom of the water and lie there.

As the **mouth opening** does not form until two to five days after hatching, the tadpole naturally cannot take in any food from the outside, and so is still dependent upon the undigested yolk within its body.

So soon as the tadpole begins to take in food from the outside, the suckers deteriorate and disappear. From this time on the tadpoles are very active. They feed on almost any plant

If the temperature is higher than normal, such as it usually is in the laboratory, then the larvae may hatch in five days. In either case, however, **suckers** (Figs. 316, 317, 318) are formed in the head of a tadpole by which it attaches itself to a jelly-like substance surrounding the eggs, although it may attach itself to other objects in the water as well. Sometimes the tadpoles will even fall to the

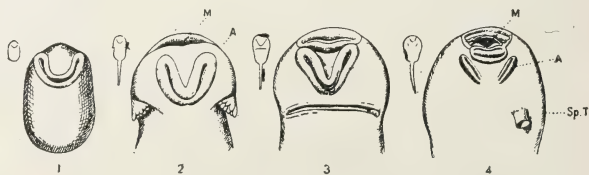


Fig. 317.

Four stages of the development of the adhesive apparatus (suckers) of *Bufo vulgaris*; *A.*, suckers; *M.*, mouth; *Sp.T.*, spiracular tube. In 3 the gills are almost completely hidden by the united right and left opercular folds.

The small outline figures indicate the shape and approximate size of the tadpoles. (After Thiele.)

or animal debris, and in the laboratory will thrive on a diet of cereals. As the egg is dependent upon temperature for its rate of speed in developing, so the rate of speed at which the tadpole grows is dependent upon the quantity of food it obtains.

**External gills** used as **respiratory organs** develop shortly after hatching. These disappear as soon as the mouth opens, and the **true internal gills** are formed. When the true gills form, they are protected by a cover, called the **operculum**. The portion underneath the operculum remains connected with the outside by only a **single pore** on the left side, known as a **spiracle**. The limb-buds appear normally at about four or five weeks, although in the laboratory, at a higher temperature, much sooner. The anterior pair develop within the opercular cavity, and consequently cannot be seen from the outside. The posterior develop, one on each side of the cloaca a little later, and become quite large and jointed by the end of the second month.

In the meantime the lungs have been growing, and the young tadpole comes to the surface of the water to expel small bubbles of air and to take in a fresh supply. In the common species of frogs, metamorphosis begins at about the end of the third month. It is at this time that the tadpole ceases feeding, and the outer layer of skin, as well as the horny jaws (Fig. 318), are thrown off. The lips shrink, the mouth is no longer suctorial and becomes much wider, while the tongue increases in size. The eyes also become prominent. The fore-limbs appear, the left one pushing through the opening of the gill chamber, while the right pushes its way through the opercular fold on that side, leaving a ragged hole. The stomach and liver enlarge, while the intestine becomes shorter and smaller in diameter than before, and the animal becomes carnivorous. The gill-clefts close and many changes occur in the blood vessels due to the change in the animal's mode of breathing. The bladder is formed, the kidneys undergo changes, and there is a definite sexual differentiation. The tail shortens and is finally lost as the hind legs continue to lengthen.

If, however, the water has been particularly cold, the metamorphosis may be put off until the following spring; in fact, it seems normal with some species to wait even longer than this, namely, as long as two years, and sometimes three (*Necturus*) before the adult form is assumed.

A frog's egg is somewhat akin to a chicken's egg which has been laid without a normal shell. The yolk is a rather blackened mass with a jelly-like substance surrounding it, similar to the white of the hen's egg, but without a solid shell. Great masses of the eggs are found in one place, appearing very much as though dozens of hen's eggs were

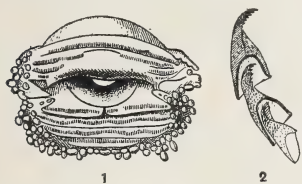


Fig. 318.

1, Front view of the mouth of a tadpole of *Rana temporaria* showing the transverse rows of tiny horny teeth; 2, Three successive horny teeth highly magnified. (After Gutzeit.)

broken, but with the yolks entire. The eggs vary in different species from one and five-tenths millimeters in diameter to twice that size. A little over half of the egg is quite black, due to the pigment granules contained therein, while the remainder is rather white although, again, in different species the quantity of pigment may vary greatly. The darker portion is commonly known as the **animal pole** and the lighter the **vegetal pole**.

There are three membranes covering the egg: **primary**, that known as the **vitelline membrane**. This can sometimes be distinguished from the pigmented substance lying directly beneath it although some writers deny that it exists at all.

The **secondary membrane** (sometimes called the **chorion**) is a rather thin but tough layer secreted from the follicle cells of the ovaries.

The **tertiary membrane** is a thick jelly-like layer derived from the walls of the oviduct, lying close to the chorion, first as a dense layer, but later, as it enlarges, it becomes quite clear.

It will be remembered that the yolk granules were quite evenly distributed in the yolk of the hen's egg and that the embryo developed upon the yolk. In the frog, however, the **deutoplasm**, or food part of the yolk, all lies at one end—the vegetal pole. Frog's eggs are, therefore, said to be **telolecithal**.

The nucleus lies in the animal pole and has already begun to divide by the time the egg is laid. In fact, it is already in the metaphase of the **second polar division** at that time. The first polar body has been thrown out and can be seen as a very tiny light spot in the flattened area of the upper pole.

As the reproductive organs of the adult have just been reviewed we shall not again discuss them here; the **development** of these organs will be taken up individually at a little later period. The general development of egg and sperm are quite like that which occurs in the germ cells of the chick.

## FERTILIZATION

The sperm drills its way through the thin jelly of the chorion and normally enters the egg substance in the pigmented region. The point of entry is a meridian passing through both poles of the egg. The meridian which passes through the animal and vegetal poles of the egg, as well as through the point where the sperm enters, is called the **fertilization meridian**. Only one sperm normally enters the egg. Polyspermy is not, however, rare, but so far as we know, always results in some abnormal development when it takes place.

It will be remembered that, after one-half of the chromosome material of the nucleus of the egg has been thrown out by the two polar divisions, the nucleus, which then contains **one-half the normal number of chromosomes**, is called the **female pro-nucleus**. The head of the sperm

(which also has only half of the normal number of chromosomes) now enters the egg and leaves a trail of pigment behind it. This sperm, after entry into the egg, becomes the **male pro-nucleus**. The head of the sperm makes its way directly to the female pro-nucleus. The tail of the sperm is thrown off although both tail and midpiece enter the **penetration path** (Fig. 319). The head and midpiece, after traveling for some distance in the egg, rotate so that the midpiece is placed in advance of the head. The midpiece then begins to dissolve and to form a typical nucleus with an opening within. This opening is called a **vesicle**. The sperm then changes its course and moves toward the point where male and female pro-nuclei will unite, unless, of course, the penetration path has already led in that direction. The path made by the changing of direction of the head of the sperm is called the **copulation path** (Fig. 319). This path is also marked by a trail of pigment as the head of the sperm passes through the cytoplasm to reach the female pro-nucleus.

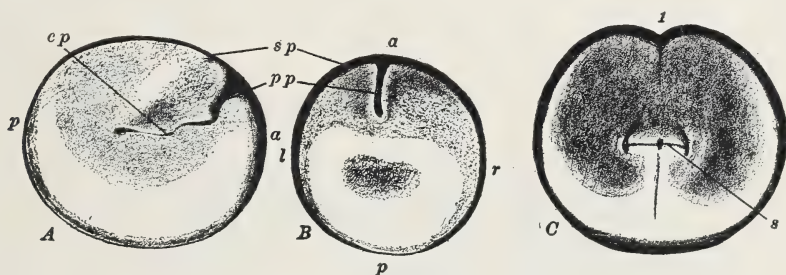


Fig. 319.

Sections through the egg of *R. fusca*, showing penetration and copulation paths, and the symmetry of the first cleavage plane. *A*, Sagittal section through the egg before the appearance of the first cleavage; *B*, Frontal section of the same stage as *A*, showing the symmetrical distribution of the egg material. *C*, Frontal section through egg in two-cell stage, showing the symmetry of the egg; the penetration path is not shown. *a*, Anterior; *cp*, copulation path; *l*, left; *p*, posterior; *pp*, penetration path; *r*, right; *s*, remains of first cleavage spindle; *sp*, superficial pigment; *l*, first cleavage furrow. (After O. Schultze.)

After the sperm has entered the egg, some of the fluid from the egg proper is withdrawn into a space **between the egg itself and the chorion**. This is known as a **perivitelline space**. The egg can thus rotate within its membrane. From this time onward the pigmented pole is always uppermost. In unfertilized eggs, the membranes are more or less adherent. The jelly-like covering of the egg absorbs considerable fluid and swells up in about a minute after the egg touches water. A close observation of the jelly shows that it is made up of various layers whose function is not only to protect the egg from chemical and mechanical injuries and from being eaten by other organisms, but also to elevate the temperature of the egg. They accomplish this latter by being transparent spheres which condense the heat rays from the sun and at the same time check the radiation from the egg itself.

## MATURATION

It has been stated that by the time the sperm enters the egg, the second polar division has already taken place, or rather, the metaphase of the **second division is in the process** of taking place. This division is completed rapidly and cuts off the second polar body in about thirty minutes after the sperm enters the egg. The second polar body is either the same size or smaller than the first. The egg-nucleus then assumes its usual form. The polar bodies are often seen floating about in the perivitelline space.

The male and female pro-nuclei now move toward the center of the egg and meet in the usual manner. The female pro-nucleus does not leave any pigment in its trail as does the male. The sperm centrosome and centrosphere divide to form the poles of a small but typical cleavage figure which is always located toward the animal pole; never in the center of the egg.

Immediately after fertilization there is a **streaming of the formative protoplasm** upward and the deutoplasm downward so that the animal pole obtains practically no yolk and the vegetal pole is composed almost entirely of it. At this time also, the pigment granules, directly opposite the point where the sperm enters the egg, are carried away leaving a somewhat crescent shaped lighter area. This crescentic area extends from half to two-thirds the distance around the egg and is known as the **gray crescent** (Fig. 320). This moving of the heavier portion to one side changes the specific gravity of the egg so that the portion possessing least weight lies uppermost and close to the gray crescent just opposite the point of entry of the sperm.



Fig. 320.

Frog's eggs showing formation of gray crescent from side and from vegetal pole.  
The animal pole is heavily pigmented.

In about an hour and a half after the entrance of the sperm, in *Rana fusca*, according to Bracheti, the egg has arranged itself in the manner described, and is now ready for the first cleavage. A vertical plane is drawn through the point where the sperm enters the egg and passes over the top of the egg through the egg-crescent. This becomes the midline on both sides of which the bilateral embryo is to develop.

There are three distinct substances of varying specific gravity in the frog's egg, namely, **protoplasm**, **pigment**, and **deutoplasm**. These

do not arrange themselves in the manner described until **after fertilization**, so that we may say that bilateral symmetry in the frog's egg is **potential but not actual until after fertilization** and the rearrangement of these three different substances.

The original cleavage plane lies at right angles to the **egg axis**, but not at right angles to what is to become the axis of the embryo itself. There is no direct relation between the plane of the first furrow in cleavage and the fertilization meridian. The midline of the developing embryo and the penetration path of the sperm normally correspond to a vertical plane known as a **gravitational plane**, drawn through the egg after the particles of protoplasm and deutoplasm have rearranged themselves according to gravity. All of these correspond to the first cleavage furrow, though many variations of this occur.

### THE FORMATION OF THE BLASTULA

One of the chief reasons for studying the embryology of the chick before that of the frog is that the **three germ layers** of the chick are more readily seen. The frog's egg divides into two portions, then into four, eight, etc., quite like the hen's egg, and by the time there are eight cells present, the four cells in the region of the animal pole are found

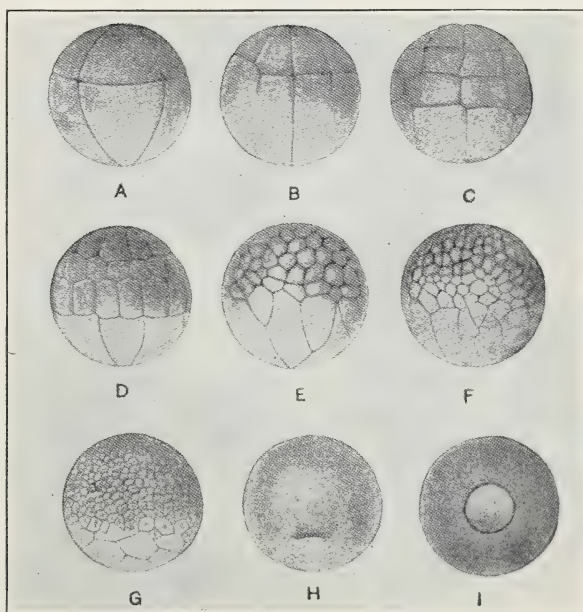
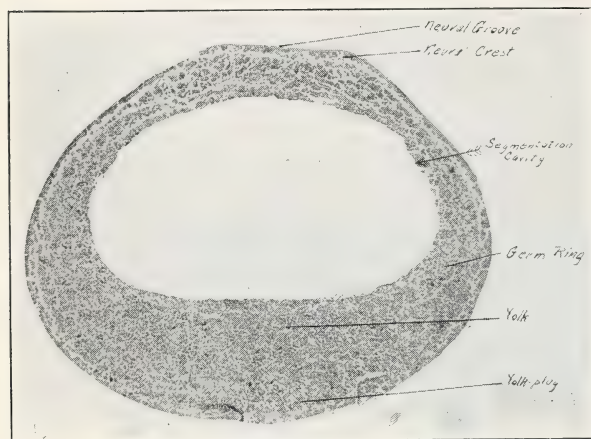
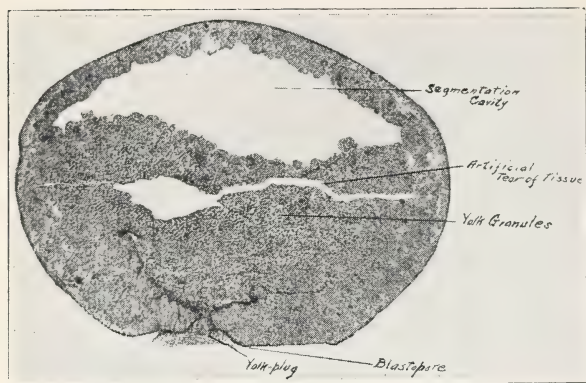


Fig. 321.

Cleavage of the frog's egg. *A*, Eight-cell stage; *B*, beginning of sixteen-cell stage; *C*, thirty-two-cell stage; *D*, forty-eight-cell stage (more regular than usual); *E*, *F*, *G*, later stages; *H*, *I*, formation of blastopore. The central light area in *I* is the yolk-plug while the ring which encases the yolk-plug is the margin of the blastopore. (After Morgan.)



to be smaller than the four in the region of the vegetal pole. The smaller ones are called **micromeres** and the larger ones **macromeres**. The micromeres, after the fifth cleavage begins, divide more rapidly than do the macromeres. By a continually more rapid growth of this kind, the smaller animal cells soon almost surround the vegetal or yolk substance. As the yolk becomes surrounded more and more, there is a somewhat central region where the yolk can still be seen from the exterior. This portion of the yolk is called the **yolk-plug**, while the margin of darker animal cells immediately surrounding the yolk-plug is called the **blastopore** (Figs. 321, 323).

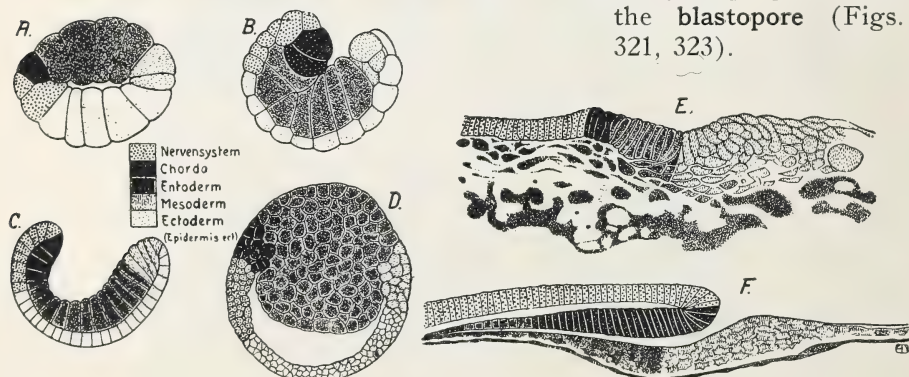


Fig. 322.

First two figures, photographs of Frog Blastulas. *A* to *F*, median sections through Blastulas and Gastrulas of *A. Cynthia bipartita* with 64 cells (this is a member of the tunicates). *B*, Gastrula of *Ciona intestinalis* (also a tunicate). *C*, Gastrula of *Amphioxus*; *D*, Blastula of *Axolotl* (Mexican salamander which breeds in the larval stage); *E*, Gastrula of an early stage of Turtle (*Chelonia caonana*), *F*, gastrula of a later reptilian stage (in the *Gecko*), (*A* to *F* after Babl and Van Beneden).

The fact that the entire yolk comes to lie **within** the blastoderm, causes much of the growth process to be hidden from view. In fact, Professor Johnstone of Cambridge University suggests that the frog embryo may not have the three regular germ layers at all. We think they are present although pressed together so closely that it is practically impossible to distinguish them.

A slight separation of the darker cell layer in the yolk-plug region leaves an opening called the **segmentation cavity** or **blastocoele** (Figs. 322, 323). The portion of the **pigmented layer**, which has separated from the yolk-plug, will now be known as the **dorsal lip of the blastopore** (Fig. 323).

The segmentation cavity forms near the animal pole. The entire blastula, however, is not much larger than the original egg because, although there are now thirty-two to sixty-four cells definitely formed, these have been formed by constant cell division **without much growth** after dividing. The roof and walls of the segmentation cavity are, therefore, composed of the external pigmented animal cells. These cells are of different shapes and sizes, rather irregular and loosely arranged, and really divided into two sheets, one lining the blastocoele while the other forms the true outer layer of the blastula. It will thus be seen that the frog blastula is not made up of a single layer of cells but of a **double**

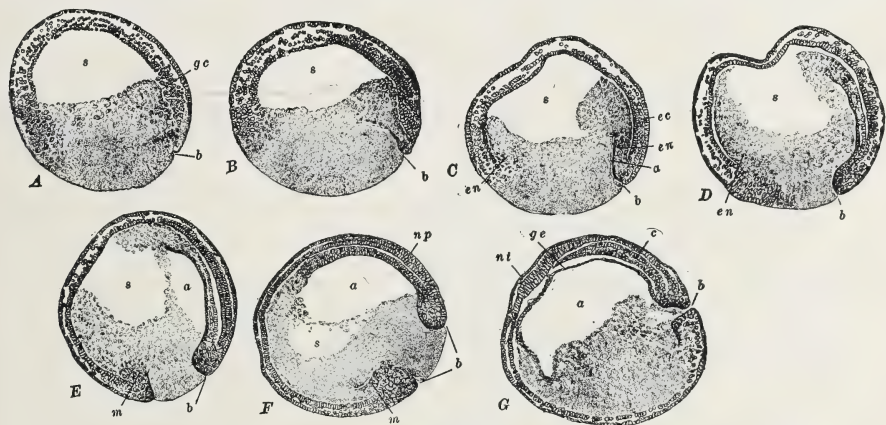


Fig. 323.

Median sagittal sections through a series of gastrulas of the frog (*R. temporaria*). The figures illustrate the change in position of the whole gastrula, as well as the phenomena of gastrulation proper. *A*. Commencement of gastrulation; earliest appearance of the dorsal lip of the blastopore. Internally the gastrular cleavage is indicated. *B*. Invagination more pronounced; beginning of epiboly. *C*. Invagination, epiboly and involution in progress. The gastrular cleavage is now indicated on the side opposite the blastopore. Rotation of the gastrula. *D*. Just before the ventral lip of the blastopore reaches the median line. The indentation of the wall of the segmentation cavity is an artifact. *E*. Blastopore circular and filled with yolk plug. Gastrula beginning to rotate back to its original position. Peristomial mesoderm differentiating. *F*. Segmentation cavity nearly obliterated. Neural plate established. *G*. Gastrulation completed. *a*, Archenteron; *b*, blastopore; *c*, rudiment of notochord; *ec*, ectoderm; *en*, entoderm; *gc*, gastrular cleavage; *ge*, gut endoderm; *m*, peristomial mesoderm; *np*, neural plate; *nt*, transverse neural ridge; *s*, segmentation cavity or blastocoele. (After Brachet.)

**layer of animal cells.** This double layer is the **ectoderm**. The floor of the blastocoele is made up of the large vegetal cells.

As the pigmented animal micromeres divide more rapidly from now on, they naturally must grow toward the equator. This causes a thinning of the roof but a thickening of the walls of the segmentation cavity. The equator of the blastula seems to be the region in which the cells multiply most rapidly, and this equatorial region is called the **germ-ring** or **growth zone** (Fig. 324).

At the time when the germ-ring begins its rapid multiplication of cells, the gray crescent extends downward rather rapidly. This region is to become the **posterior**, or **caudal**, side of the embryo. The germ-ring from now on continues extending beyond the equator into the vegetal region until it lies approximately half way between the equator and vegetal pole. This growing of the germ-ring pushes the yolk more and more within the overgrowing animal cells as already mentioned. The yolk thus being pushed within, naturally forces the floor of the segmentation cavity into a convex arch.

This is considered the **end of blastulation** in the frog's egg.

### THE FORMATION OF THE GASTRULA

We have at this point, then: most of the yolk withdrawn within the overgrowing animal cells, two layers of which form the outer covering of the blastula at the animal pole; a segmentation cavity with its floor convexly arched; and a definite antero-posterior differentiation, the posterior side being marked by the gray crescent.

The development of the gastrula begins just beneath the posterior lip of the blastopore by a groove which forms directly between the animal cells and the yolk cells (Fig. 323, A, gc). The groove itself is lined by both kinds of cells on its opposite faces. We know from the development which takes place later that this groove is the real beginning of **invagination**. The groove itself becomes the **archenteron** or **primitive intestinal tract** (Fig. 323, C, E, F, G, a). The upper lip of this groove is the **rim of the blastopore** (Fig. 323, b). The animal cells become the **ectoderm** and the yolk cells become **entoderm**.

As the yolk is pushed within the blastula it causes a narrow groove to form in the region of the blastocoele. This groove separates the rising floor from the remaining yolk and finally becomes a definite narrow slit which splits off the ectoderm and entoderm at the point of invagination. The original groove is known as the **gastrular groove**, and the splitting off into ectoderm and entoderm is called **gastrular cleavage** (Fig. 323, A, gc). This gastrular cleavage extends from the dorsal lip of the blastopore entirely around the gastrula to the opposite side from where invagination takes place.

In the invagination area a definite tongue of ectodermal cells pushes inward (Fig. 323, C, en) to join directly with the inner yolk cells to

form the entoderm. Due to their position, the inner yolk cells are also entoderm, although they do not form by a true invagination.

Viewing the entire egg externally, during the process of gastrulation, we may consider the germ-ring as something like a rubber band placed about an ordinary ball in an equatorial plane. By sliding the rubber band off the ball toward one side, we may understand how the germ-ring brings its lateral region together in the mid-rim in the posterior or caudal region. This coming together not only pushes the underlying cells within, but causes the entoderm to extend further inward and thus increases the cortical extent of the archenteron.

We, therefore, have the first invagination of the pigmented cells forming the dorsal lip of the blastopore; the invagination then extends laterally in both directions to form the **lateral lips of the blastopore**; and finally the process of invagination continues around to the side of the gastrula, practically to a point almost opposite to where it began, and where the **ventral lip of the blastopore** is formed. This completes the **entire blastopore**. After the yolk plug has disappeared within the gastrula, the blastopore remains a narrow, elongated slit connected with the archenteron.

The method by which the blastopore grows by **concrecence** to form the **primitive streak** has already been described in the case of the chick, a rereading of which should be done at this point. Comparisons should constantly be made between the development of frog and chick embryos.

It will be noted from what has been said that gastrulation is not so much formed by invagination in the frog as it is by a **delamination** within the gastrula itself.

In fact, among the higher chordates, invagination is sometimes entirely lacking, so that gastrulation may be accompanied by either **involution**, such as takes place in the chick, or by **epiboly**, which occurs to some extent in the frog, and by **delamination**, a process just described.

At this point Figures 321, 323 must be studied to understand the varying changes of positions of the blastopore brought about by the rotation of the egg. It is also to be remembered that the blastopore marks the caudal extremity of the embryo.

The two-layered stage in the frog is of very short duration.

In the inner region, where the germ-ring and the yolk-cells which line the blastocoele are continuous, there are **transitional cells** which are to become the **mesoderm** (Fig. 324, m). These cells are continuous with ectoderm on one side, and entoderm or yolk-cells on the other, and can not be distinguished as definite mesodermal cells until the blastopore is completely formed.

In other words, the mesoderm first appears as a ring of cells just **within the margin of the blastopore**. This mesodermal region is broadened considerably in the dorsal region.

As the blastopore closes, it carries mesodermal cells toward the mid-line (Fig. 324) to form a broad median band extending forward from the dorsal lip of the blastopore. These cells then multiply and, as the dorsal lip extends downward, an **axial thickening** is formed. At this same time the archenteron extends and carries yolk-cells outward toward the animal pole so that the extent of the mesoderm is almost as great as that of the entoderm.

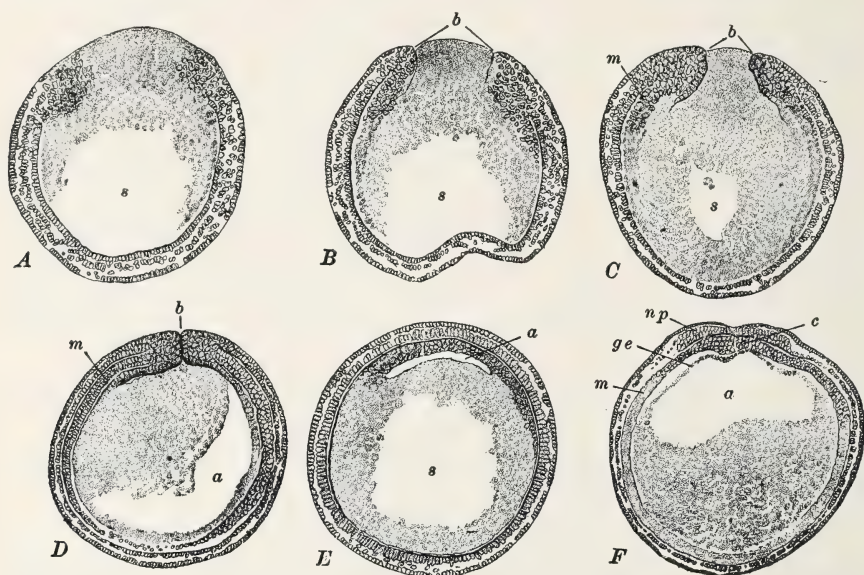


Fig. 324.

Frontal and transverse sections through gastrulas of the frog (*R. temporaria*) of various ages. *A*. Frontal section through gastrula of same age as Fig. 323. *C*. *B*. Frontal section through gastrula of same age as Fig. 323. *D*. *C*. Frontal section through gastrula slightly older than Fig. 323. *F*. *D*. Frontal section through gastrula of same age as Fig. 32. *G*. *E*. Transverse section through gastrula slightly older than Fig. 323. *G*. *F*. Transverse section through gastrula slightly older than Fig. 323. *a*, Archenteron; *b*, blastopore; *c*, notochord; *ge*, gut endoderm; *m*, peristomial mesoderm; *np*, neural plate; *s*, segmentation cavity or blastocoele. (After Brachet.)

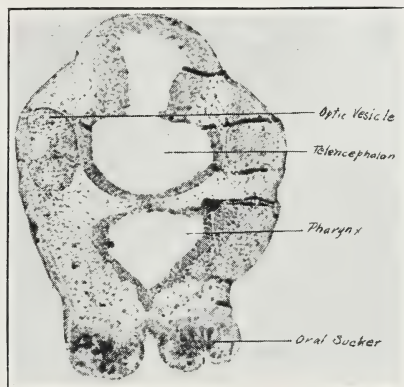
Then a rearrangement of cells takes place so that an irregular delamination begins in the dorsal lateral regions on each side of the thickened axial mass. This delamination extends from there anteriorly and laterally around the sides of the archenteron. Thus a thick layer of mesoderm is formed between the entodermal lining of the archenteron and the outer ectoderm (Fig. 324, *m*).

At the lower pole, that is, toward the place where the yolk-plug is being drawn into the interior of the egg (Fig. 324, *b*), the lower surface of the yolk is also delaminated so that a circular margin of the mesoderm is formed there. It is from this layer of mesoderm that cells and groups of cells bud off and pass toward the lower pole—it is to be remembered that these cells and groups of cells begin their growth in the **lower pole**

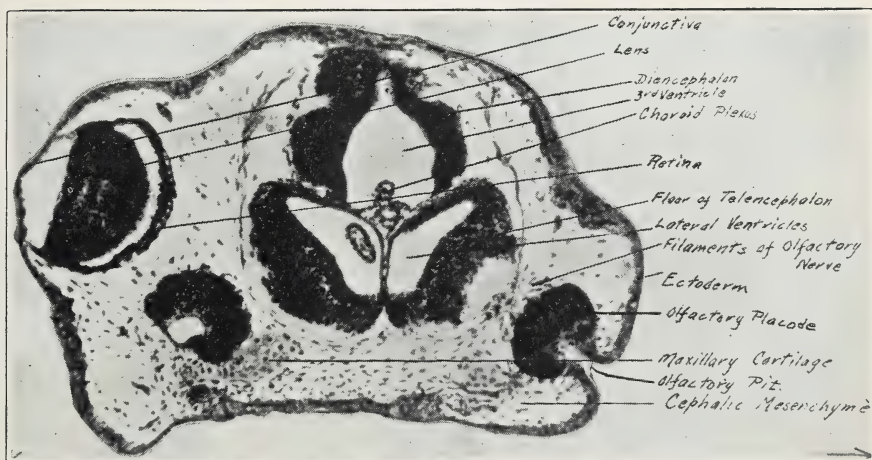
region, but lie above the lower pole itself)—toward the ventral portion of the blastopore, so that a more or less completely continuous layer of mesoderm is formed between the ectoderm and entoderm.

In the dorsal region of the blastopore, and extending along the dorsal axial mass, delamination does not occur as rapidly as in the ventral region. The course of delamination is also modified here. This modification is no doubt due to the fact that in this dorsal axial region the cells, which are to become mesoderm, are derived from the cells which **invaginated** from the outer layer, while in other regions this is not the case. Then, too, it is in this region that the notochord forms, which further complicates matters.

In fact, cross sections in the region of the blastopore do not show



A

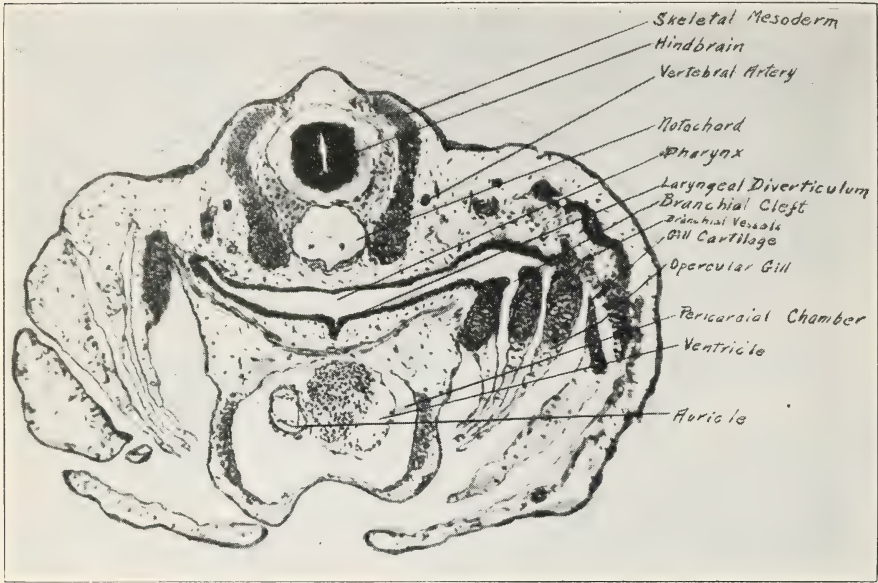


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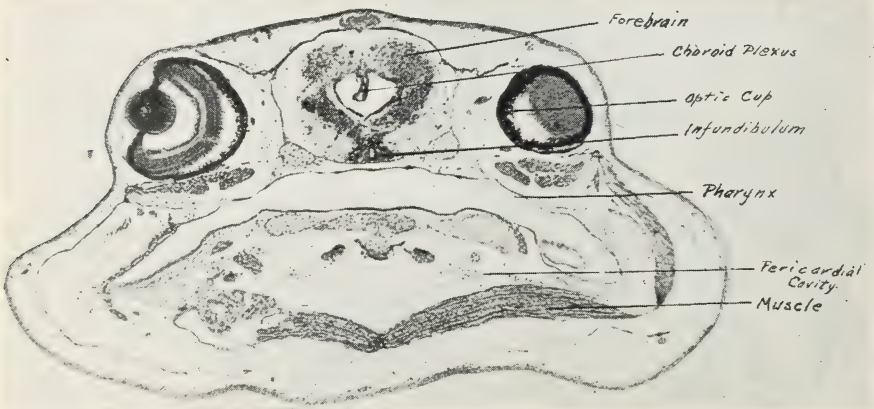
Fig. 325.

A, B, C, Transverse sections of *Amblystoma* tadpole. A, through suckers; B, through optic and olfactory region; C, through gill region.

lines of demarcation between the notochord, mesoderm, and the dorsal entoderm for some little time; but sections through the blastopore (while the yolk-plug is still protruding) show the rim of the blastopore to be composed of thick, undifferentiated cells which are a part of the contracted germ-ring. A little laterally, the ectoderm is separated by a narrow space or line which has formed during gastrulation, and the



C



D

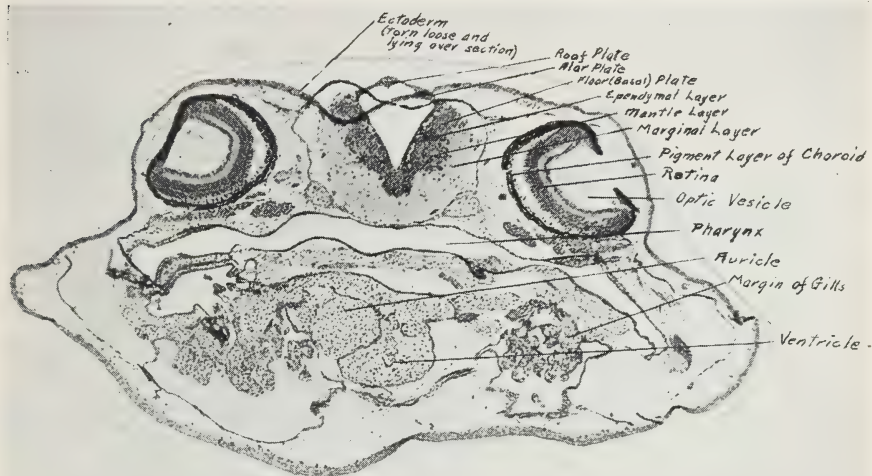
Fig. 325.

D, E, F, Photographs of transverse sections through 12 mm. frog tadpole. The sections are cut diagonally; the left eye (right side of figure) lying more cephalad, is the most anterior. E, immediately posterior to D, but lens was lost in sectioning; F, immediately posterior to middle cut.

thin entoderm is separated from the middle layer. This separation of layers is the **delamination process** we have been discussing.

As the **outer animal cells are pigmented**, we assume that whenever pigment is found in any of the inner cells, it is an indication that such pigmented cells are derived from the ectoderm.

As the yolk-plug is withdrawn, the blastopore becomes a mere slit, and the ectoderm and mesoderm separate considerably and dip downward toward the entoderm in the dorsal midline although never so far



E



F

Fig. 325.

as to reach the entoderm. This leaves a narrow, vertical ridge of cells at the midline.

A pair of slight depressions from the archenteron appear only as virtual grooves formed by pigmented cells. Forward from this, the lower margins of these grooves come to look like lips which approach the midline. The mesoderm in the meantime separates from the archenteron to a considerable extent (Fig. 324).

Still farther forward, the grooves disappear, while the spaces between mesoderm and entoderm, as well as between mesoderm and ectoderm, extend vertically and delimit the pair of mesoderm masses.

The cells thus left in the midline between the mesodermal sheets form a wedge-shaped elevation which is continuous with the entoderm. This is the **beginning of the notochord**. (Figs. 323, G, c, and 324, F, c).

The notochord is now cut off from the entoderm by a narrow slit which leaves the archenteron with a dorsal roof, one cell in thickness. (Fig. 324.)

From this point, posteriorly (toward the blastopore), the grooves of the archenteron are better marked.

### THE MEDULLARY PLATE

At the same time that the notochord is developing, the medullary plate is also being formed (Figs. 324, np, and 326, everything above mes.), partly from the medial band of cells which extends from the region of the dorsal lip of the blastopore nearly to the animal pole, and partly from the axial thickening caused by the confluence of the lateral portions of the germ-ring.

The inner portion of the former region is called the **nervous layer** of ectoderm. It is this nervous layer which begins to thicken. By the time the blastopore has begun to close, a thickened medullary plate has formed over the entire dorsal surface of the gastrula, essentially like that described in the chick.

At about the time the yolk-plug has disappeared, the lateral ridges have become elevated to form the **lateral neural ridges** (Fig. 327, n, f).

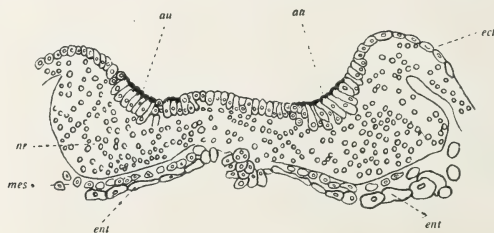


Fig. 326.

Transverse section through frog tadpole in the anterior region of the neural groove. *au*, eye-pits. (Note the pigment in the outer cells); *ect*, outer layer of ectoderm; *ent*, entoderm; *mes*, mesoderm; *nr*, anlage of the neural crest. (After Eyclesheymer.)

These extend from the blastopore to almost directly opposite on the dorso-lateral portion of the embryo. Here they turn sharply to pass toward the midline where they meet to form the **transverse neural fold**. It is this latter fold which marks the anterior limit of the medullary plate. The median groove becomes more pronounced and is then called the **neural groove**.

The important points to bear in mind here are:

**First**, that, as in the chick and all chordate animals, so too in the frog, the closing of the blastopore by confluence (extending in an antero-posterior direction, on the dorsal aspect of the embryo) forms a definite

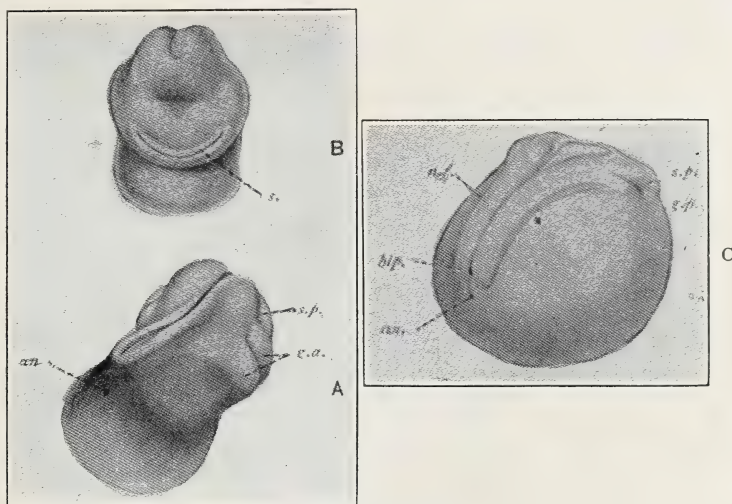


Fig. 327.

Frog embryos. *A*, from behind and above; *B*, from in front; *C*, slightly earlier than *A* and *B*. *an.*, proctodeum (the invagination from which anus will form); *blp.*, blastopore; *ga.*, gill arches; *gp.*, gill plate; *nf.*, neural fold; *s.*, sucker; *sp.*, sense plate. (After Borradaile.)

axis, which means that by this confluence, the germ-ring becomes the axis. It is on each side of this axis that organs and important structures develop.

**Second**, that **gastrulation** involves only the forming of two layers (ectoderm and entoderm) from the single layered blastula.

**Third**, that **notogenesis** includes all the processes involved in the formation of the medullary plate, notochord, and mesoderm.

Gastrulation is accomplished in the frog chiefly by a delamination and rearrangement of the yolk cells and only to a slight extent by invagination. The process of invagination is chiefly concerned in forming the beginning of the notochord and the mesoderm in the dorsal and dorso-lateral regions. These latter structures are not formed entirely, however, by invagination, but also by material from the germ-ring which

has been carried to the axial region. Invagination, in the frog, is therefore considered of minor importance.

**Amphioxus** is the only chordate which remains in a two-layered state for some time. All other chordates retain this condition for a short period; this is so because the mesoderm begins its development almost at the moment of gastrulation.

In fact, in the frog, mesodermal cells are found almost immediately after the entoderm cells **begin** to form. They are found, first, all around the margin of the blastopore where they form an important part of the germ-ring. Mesoderm which forms in this way is called **blastoporal** or **peristomial**.

As confluence begins, the lateral portions of the germ-ring are brought closer to the mid-dorsal region where they become a part of the axis of the elongating embryo. That is, they form the mesodermal bands, already referred to, and it is these bands of the germ-ring which become **axial in position**, then to be known as **gastral mesoderm**. This gastral mesoderm is nothing more nor less than mesoderm derived in turn from the blastoporal mesoderm. It is no different from any other mesoderm derived from the same origin, although it lies, of course, in a different position from the remaining mesoderm. Regarding **Amphioxus**, however, the above statement would not be true; for, in that animal, gastral mesoderm and blastoporal mesoderm have different origins. This difference in origins may be traced to the fact that in the frog the mesoderm differentiates **before** gastrulation and confluence, while in **Amphioxus**, the mesoderm does not differentiate until **after** these two processes have begun.

## THE FORMATION OF THE EMBRYO

All that has been discussed so far has taken place within two days after fertilization. Now the embryo can be seen either lying in a straight line, or slightly concave, on the dorsal surface. The ventral surface appears convex. The ectoderm still forms the entire covering epithelium, although some of these ectodermal cells have developed cilia which appear just before the fusion of the neural folds. These cilia beat in a posterior direction to give the embryo a slow rotary motion within the egg membranes.

The **transverse neural fold** marks the anterior limit of the nervous system, while the posterior limit is located just anterior to the dorsal lip of the blastopore.

As confluence continues, the nervous system comes to extend from almost pole to pole on the posterior surface of the gastrula, even before the blastopore has entirely contracted. The gastrula then rotates so that this posterior portion becomes dorsal; this brings the transverse neural fold to the anterior end of the nervous system, while the medullary plate occupies nearly the entire dorsal surface of the embryo.

The ridges which form on the neural plate, and later fuse in a similar manner to that described in the chick, begin fusion in the region of the medulla (Fig. 327) and continue both anteriorly and posteriorly. The transverse fold extends backward to form the roof of the expanded brain end of the developing nervous system. It meets the lateral folds in the region lying between the fore and mid-brain and as it is the last region of the neural tube to close, it is called the **neuropore**. The neuropore lies just posterior to where the **epiphysis** is to appear. It is quite transitory.

Neural crests are formed in the way they were formed in the chick embryo.

The blastopore has become a narrow slit, the lateral walls of which fuse, leaving two openings, an upper and a lower. The upper one is directly continuous with the archenteron while the lower one is known as the **proctodaeum**. The proctodaeum is but a slight depression lined with ectoderm.

The posterior ends of the neural folds extend out from the middle regions where they fuse, to form the neural tube which then covers the upper blastoporal opening, thus forming a connection between arch-

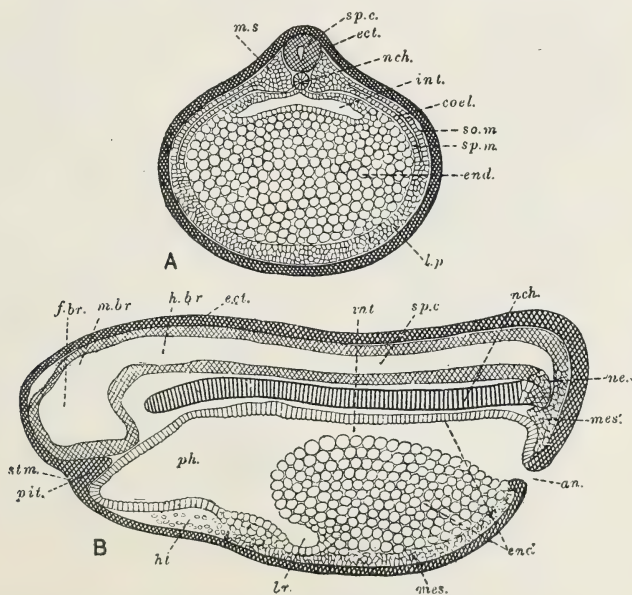


Fig. 328.

Sections of an embryo frog. *A*, transverse; *B*, longitudinal. *an.*, Anus; *cwl.*, cœlum; *ect.*, ectoderm or epiblast; *end.*, endoderm or hypoblast; *f.br.*, fore-brain; *h.br.*, hind-brain; *ht.*, rudiment of heart; *int.*, intestine; *l.p.*, lateral plate of mesoblast; *lr.*, rudiment of liver; *m.br.*, mid-brain; *m.s.*, mesoblastic somite; *mes.*, mesoblast; *mes'*, mesoblast continuous with epiblast of neural canal and hypoblast of notochord; *me.c.*, neurenteric canal; *nch.*, notochord; *ph.*, pharynx; *pit.*, rudiment of pituitary body; *so.m.*, somatic mesoblast; *sp.c.*, spinal cord; *sp.m.*, splanchnic mesoblast; *stm.*, stomodæum. (After Borradaile.)

enteron and neural tube. This opening is called the **neurenteric canal**. (Fig. 328.)

Just as with the chick, the confluence of the two lateral walls of the blastopore (which have been formed from the remains of the germ-ring) bring a median cell mass together in the axial region, in which ectoderm, entoderm, and mesoderm are fused in a quite undifferentiated mass. This is the **primitive streak**. The groove which lies in the mid-line of the primitive streak is called the **primitive groove**.

It is from this primitive streak that ectodermal cells are budded forth into the neural folds and upon the surface of the body. It is from the primitive streak, also, that mesodermal cells are budded off into the lateral bands, and entodermal cells into the walls of the archenteron.

At this time the chief characteristic of the brain is the **single flexure** around the tip of the notochord (Fig. 329). The **hypophysis** (pituitary body) can be seen as a tongue of ectodermal cells just beneath the end of the fore-brain; it extends inward a short distance.

The rudiments of the eyes (Fig. 326, au) are indicated as small patches of the deeply pigmented ectodermal epithelium in an antero-lateral region of the medullary plate.

The rudiments of the ears (Fig. 282, C) are seen as thickened patches of the inner or nervous layer of ectoderm opposite the region of the hind-brain. They are difficult to see externally as yet.

The rudiments of the olfactory organs are formed as thickened patches of ectoderm below and in front of the optic rudiments. The tiny depressions on the surface which are to form the future olfactory pits may sometimes be seen at this period.

The notochord is completely delaminated, except in the region of the primitive streak, by the time the neural tube has closed.

By the time the neural tube is completed, the archenteron is called a **mesenteron**; the anterior enlarged end forms the **fore-gut**, the walls of which are but one cell in thickness (Fig. 329). The fore-gut region is also called the **pharynx** in the embryo. The stomach and oesophagus are later to be developed from this region.

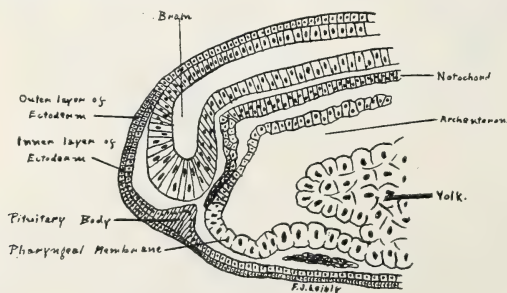


Fig. 329.

Sagittal section of Anterior end of a frog tadpole 3.6 mm. long  
(Redrawn from Corning.)

Just in front of the neurenteric canal there is also an enlargement which forms the **hind-gut** or **rectal portion** of the intestine.

The **mid-gut** is, as in the chick embryo, that small portion in direct connection with the yolk.

It will be remembered that the true mouth forms in chordates as a 'secondary inpocketing of ectoderm. In the frog, the outpocketing from the fore-gut, which is to meet the ectodermal inpocketing, is seen just below the fore-brain (Fig. 329, pharyngeal membrane). This is the region where the mouth will form later.

The liver will be seen as a ventral outgrowth beneath the anterior end of the yolk mass (Fig. 328).

In sections, the rudiments of the first two or three visceral pouches can be seen as vertical outgrowths from the sides of the pharyngeal walls (Figs. 295 and 330). The pouches extend to the ectoderm with

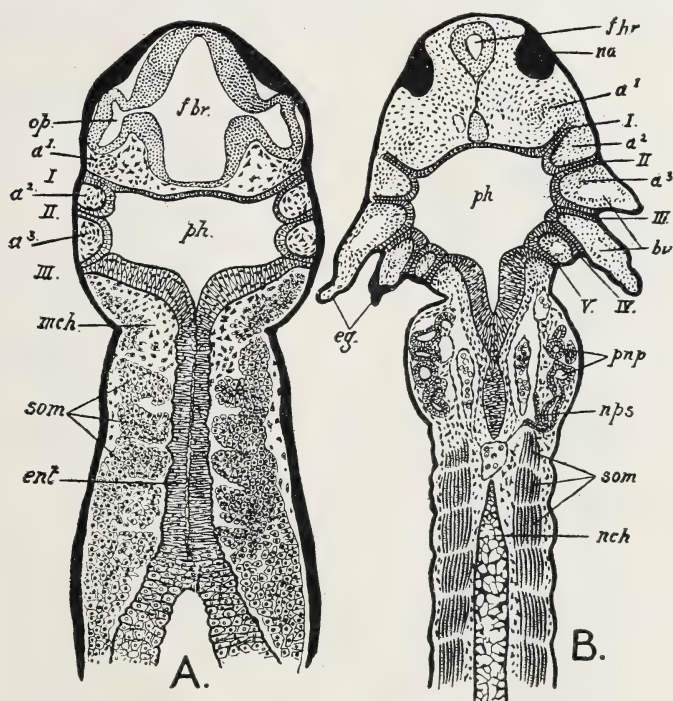


Fig. 330.

*A.* Horizontal section through an embryo frog some time before hatching, showing the optic vesicles springing from the sides of the fore-brain, the three anterior pairs of gill-slits, and five pairs of mesoblastic somites. *B.* A similar section through a tadpole shortly after hatching. The head is cut in a lower plane than in *A*, so only a small part of the anterior end of the brain appears in the section. *a*<sup>1</sup>, the mandibular arch; *a*<sup>2</sup>, the hyoid arch; *a*<sup>3</sup>, the first branchial arch; *bv*, blood-vessel in first and second branchial arch; *eg*, external gills; *ent*, enteron; *fbr*, fore-brain; *mch*, branching mesenchyme cells; *na*, nasal pits; *nch*, notochord; *nps*, peritoneal funnel; *op*, optic vesicle; *ph*, pharynx; *pnf*, pronephros; *som*, mesoblastic somites which in *B* are converted into muscle. *I*, mandibulo-hyoid slit; *II* hyo-branchial slit; *III-V*, branchial slits. (After Bourne.)

which they fuse. It is this fusion which causes the depressions in the ectoderm just back of the head on the external surface.

### THE SOMITES

Just as with the chick, somites are formed by transverse division along the dorsal portion of the embryo, except in the primitive streak

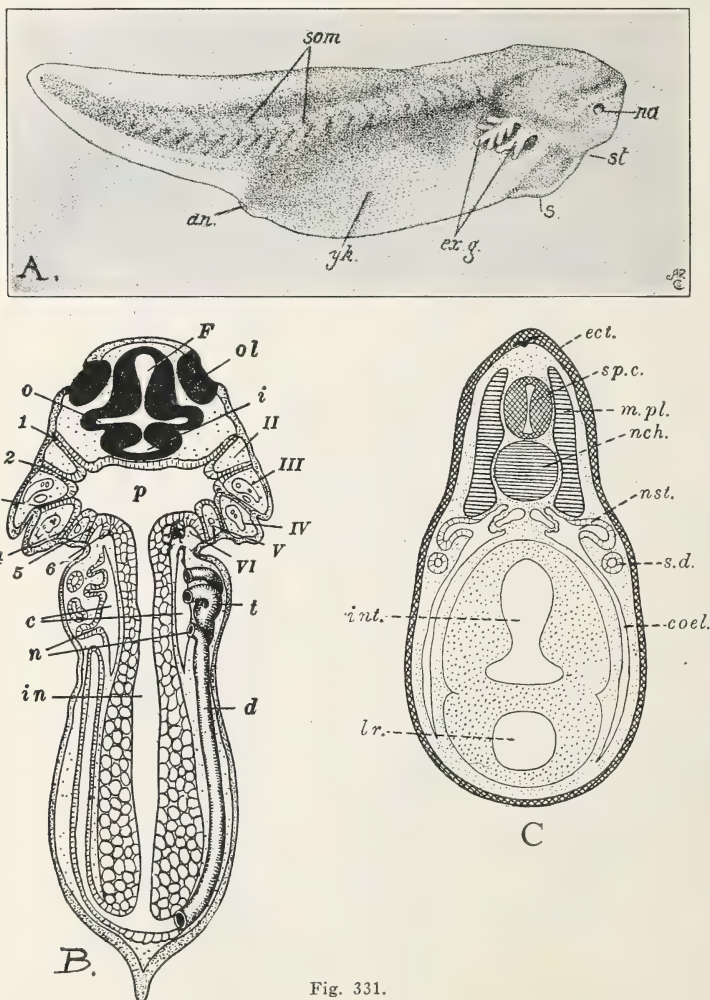


Fig. 331.

A. Tadpole of the frog at the time of hatching, *an*, anus; *ex.g.*, external gills; *na*, nasal pit; *s*, sucker; *som*, somites; *st*, stomodæum; *y.k.*, yolk-sac.

B. Diagram of a frontal section of a frog larva at the time of hatching (modified). *c*, Cœlom; *d*, pronephric duct; *F*, fore-brain; *t*, infundibulum; *in*, intestine; *n*, nephrostome; *o*, base of optic stalk; *ol*, olfactory pit (placode); *p*, pharynx; *t*, pronephric tubules; *II*, hyoid arch; *III-VI*, first to fourth branchial pouches; *I*, hyomandibular pouch; 2-6, first to fifth branchial pouches.

C. A diagram of a transverse section of the frog embryo at the hatching stage. *cœl.*, Cœlom; *ect.*, ectoderm; *int.*, intestine; *lr.*, liver; *m.pl.*, muscle plate; *nch.*, notochord; *nst.*, nephrostome; *s.d.*, segmental duct; *sp.c.*, spinal cord. The glomeruli are seen opposite the nephrostomes. (A and C, after Borradaile; B, after Marshall.)

region and in the head region. A complete sheet of mesoderm now separates ectoderm and entoderm in the embryo from the head region to the primitive streak region, and this sheet separates into two layers, an outer or **somatopleure**, and an inner known as the **splanchnopleure**. (Fig. 268.)

The thickened region, where the somites form on the dorsal surface of the embryo along the notochord, is called the **segmental plate** or **myotomal region**, while the portion extending laterally (which is much thinner) forms the **lateral plates**.

The **coelom** develops between somatopleure and splanchnopleure.

As the frog's egg has the yolk-mass **packed within** the embryo, this mass pushes the germ layers close together, so that they are by no means as clearly set apart as in the chick embryo.

Between the second, third, and fourth somites and the lateral plates, small masses of cells remain closely related to the somatopleure of the lateral plate. It is these cell masses which are to develop into the **pronephric tubules**. All of these structures must be compared with similar developmental structures in the chick embryo, at this point.

The coelom proper can be seen as a definite space only below the pharynx in front of the liver (Fig. 331). The heart will develop in the region where the loosely scattered cells are seen, ventral to the pharynx.

## THE LATER DEVELOPMENT OF THE TADPOLE

There are details in which the various species of frogs vary, but all pass through the following general method of development.

It is both interesting and profitable to call attention at this point to the fact that, while the frog was one of the earliest forms of animal life studied in the laboratory, and

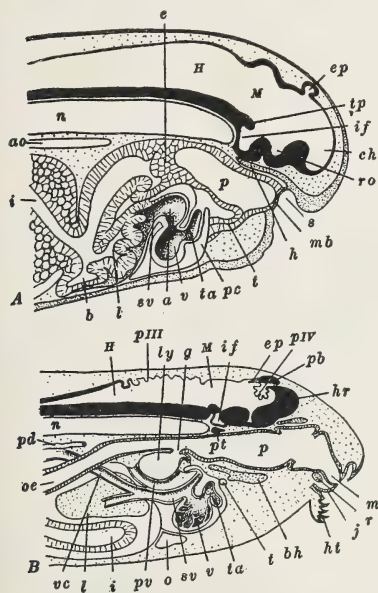


Fig. 332.

Diagrams of median sagittal sections of the anterior ends of frog larvæ. *A*. Of a larva just before the opening of the mouth. *B*. Of a 12 mm. larva (at the appearance of the hind-limb buds). *a*, Auricle; *ao*, dorsal aorta; *b*, gall bladder; *bh*, basihyal cartilage; *ch*, cavity of cerebral hemisphere (lateral ventricle); *e*, epithelial plug closing the oesophagus; *ep*, epipharynx; *g*, glottis; *h*, hypopharynx; *H*, hind-brain; *hr*, cerebral hemisphere; *ht*, horny "teeth"; *hv*, hepatic vein; *i*, intestine; *if*, infundibulum; *j*, lower jaw; *l*, liver; *ly*, laryngeal chamber; *m*, mouth; *M*, mid-brain; *mb*, oral membrane (oral septum); *n*, notochord; *o*, median portion of opercular cavity; *æ*, oesophagus; *p*, pharynx; *pb*, pineal body; *pc*, pericardial cavity; *pd*, pronephric (mesonephric) duct; *pt*, pituitary body; *pv*, pulmonary vein; *pIII*, choroid plexus of third ventricle; *pIV*, choroid plexus of fourth ventricle; *r*, rostral cartilage; *ro*, optic recess; *s*, stomodæum; *sv*, sinus venosus; *t*, thyroid body; *ta*, truncus arteriosus; *tb*, tuberculum posterius; *v*, ventricle; *vc*, inferior (posterior) vena cava. (After Marshall.)

while many hundreds of volumes and articles have been written on it from many angles, there are nevertheless hundreds of interesting points in that animal's development which are still unknown. In fact, one writer says that the gaps that confront one in the study of the frog assume "remarkable proportions" when one thinks of how much work has really been done on this much-studied animal.

Then, too, as there is no accurate method of obtaining the age of a frog, owing to the remarkable influence temperature and food play in its development, it is often difficult to make clear much that should be made clear to the student.

Roughly speaking, at the time of hatching, namely about one or two weeks after fertilization, the larvae of most species are about six or seven millimeters in length. The tadpole is usually about nine or ten millimeters in length at the time of the opening of the mouth, and eleven or twelve millimeters when the limb-buds appear.

### THE NERVOUS SYSTEM

There are no neuromeres in the brain region of the frog, though otherwise the same brain divisions take place, which we have discussed in the chick.

The **tuberculum posterius** (Fig. 332, tp) is a thickening opposite the tip of the notochord in the floor of the brain, while a dorsal thickening appears in the roof of the brain obliquely upward and forward from this. A plane passing from the tuberculum posterius in front of the dorsal thickening separates the fore-brain from the mid-brain, while a plane passing from the same tuberculum behind the dorsal thickening separates the mid-brain from the hind-brain.

The beginning of the brain divisions is quite similar to the three primary regions mentioned in the chick embryo, and a review of the matter there given will make the divisions and cavities in the frog brain understandable.

It will be remembered that the olfactory lobes and the cerebral hemispheres form the **telencephalon**, and that the telencephalon and the "tween-brain" (**diencephalon**) together form the fore-brain, while the optic lobes and optic chiasma form the main portions of the **mesencephalon**. The **cerebellum** takes up most of the **metencephalon**, while the **medulla oblongata** forms the **myelencephalon**.

### THE FORE-BRAIN

Opposite the neuropore (Fig. 328) the cells of the ectodermal cone scatter, due to the pushing out of the head tissues in advance of the brain. Soon all trace of the neuropore disappears except for a slight indentation known as the **olfactory recess**, and this also disappears a short time later.

The **lamina terminalis** (Fig. 282, C) is a thickening just below the

level of the olfactory recess in the anterior wall of the fore-brain. It extends ventrally to where the optic stalks protrude. From the drawing (Fig. 333) it will be noticed that a thickening occurs in the region of the attachment of the optic stalks to form the **torus transversus** (Fig. 333, tr) and the beginnings of the **optic chiasma** (Fig. 333, cw) and **thalami**. The torus transversus becomes the seat of the **anterior commissure** (Fig. 333, cpa) as well as other **commissures** of the brain.

The narrow depression between the thickenings just mentioned forms the **recessus opticus** (Fig. 333, ro), which is the passage to the cavities in the optic stalks.

The **infundibulum** (Fig. 333, J) is an outgrowth of the posterior portion of the fore-brain where it extends backward under the tip of the notochord.

The **epiphysis**, or **pineal body** (Fig. 333, e), is an evagination from the dorsal wall of the fore-brain at its posterior limit where the wall has become quite thin.

The **choroid plexus** (Fig. 333, pch) is the non-nervous portion of the roof of the fore-brain which has become thinned out considerably, and in which the blood vessels lie. This whole region is pushed into the third ventricle.

The **habenular ganglia** and the **habenular commissure** (Fig. 333, ch) develop between the choroid plexus and the epiphysis.

The **paraphysis** (a dorsal growth) develops in front of the habenular ganglia and commissure considerably later.

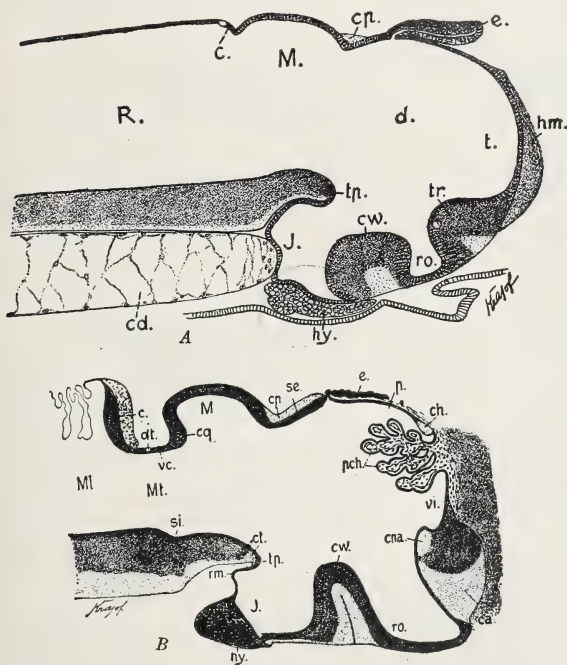


Fig. 333.

Median sagittal sections through the brain of the frog. A. Of a larva of *R. fusca* of 7 mm. in which the mouth was open. B. *R. esculenta* at the end of metamorphosis. c, Cerebellum; ca, anterior commissure; cd, notochord; ch, habenular commissure; cp, posterior commissure; cpa, anterior pallial commissure; cq, posterior corpus quadrigeminum; ct, tubercular commissure; cw, optic chiasma; d, diencephalon; dt, tract of IV cranial nerve; e, epiphysis; hm, cerebral hemisphere; hy, hypophysis; J, infundibulum; M, mesencephalon; Mt, metencephalon; p, antero-dorsal extension of diencephalon; pch, choroid plexus of third ventricle; R, rhombencephalon; rm, recessus mammillaris; ro, optic recess; se, roof of diencephalon; si, sulcus intraencephalicus (the groove which forms the hindmost boundary of the mid-brain); tn, tuberculum posterius; tr, torus transversus (telencephali); vc, valvula cerebelli; vi, ventriculus impar (telencephali) (third ventricle). (From Von Kupffer, Hertwig's Handbuch, etc.)

The cerebral hemispheres appear when the tadpole is about seven millimeters in length, that is, when it is ready to hatch.

The ventricles are similar to those in the chick.

As all these thickenings and outgrowths appear, the brain itself seems to straighten the original flexure, but this is only **apparent**, as the flexure remains, and the infundibulum still extends below and in front of the tip of the notochord.

The **hypophysis** (Fig. 333, hy) grows as an inward extension of the surface ectoderm to meet with the infundibulum.

### THE MID-BRAIN

There is not much change in this region of the brain except that the ventro-lateral walls thicken, and these thickened portions are known as the **crura cerebri**. They connect with the wall of the fore-brain. The dorso-lateral walls of the mid-brain form the large, rounded **optic lobes**.

The **posterior commissure** (Fig. 333, cp) forms the anterior limit of the mid-brain.

The **aqueduct of Sylvius** (Fig. 303) is the cavity in the mid-brain connecting the third ventricle with the cavity in the rhombencephalon.

### THE HIND-BRAIN

There is little, if any, line of demarcation in the frog which divides the hind-brain into metencephalon and myelencephalon.

The **cerebellum** (Fig. 333, c) is in the region which is commonly designated as the metencephalon. This organ is quite small in the frog, and appears late in larval life on the dorsal side of the hind-brain.

The non-nervous thinned-out roof of the fourth ventricle (which covers the dorsal part of the region of the medulla oblongata or myelencephalon); (Fig. 333, M1) forms the **choroid plexus of the fourth ventricle**.

The floor of the ventro-lateral walls of the hind-brain becomes thickened and forms the main nervous pathways to and from the nuclei of origin of most of the cranial nerves.

The brain gradually tapers into the spinal cord at the medulla oblongata.

The **central canal** is the central opening running throughout the length of the spinal cord. It is continuous with the cavities of the brain. This central canal is lined with non-nervous cells known as **ependymal cells**. The true nerve-cells, which go to make up the main portions of the wall of the spinal cord, are called **germinal cells**. These latter are in turn divided into supporting cells, or **glia cells**, and the true functional nerve cells or **neuroblasts**.

There is no dorsal fissure in the frog's spinal cord as there is in higher forms, though there is a **ventral fissure**.

The **gray matter** of the cord is formed by the neuroblasts.

## THE PERIPHERAL NERVOUS SYSTEM

The peripheral nervous system has been discussed in some detail in the chick, and will be taken up in still greater detail in our study of comparative anatomy.

In the tadpole there are some forty pairs of spinal nerves, but only ten pairs in the adult. They arise by a **dorsal and ventral root**, which unite to form the **trunk of the spinal nerve**, after which this trunk divides into a **dorsal and a ventral ramus**, while a **ramus communicans** connects the trunk with the sympathetic system.

There are also ten **cranial** nerves instead of twelve as in the higher forms.

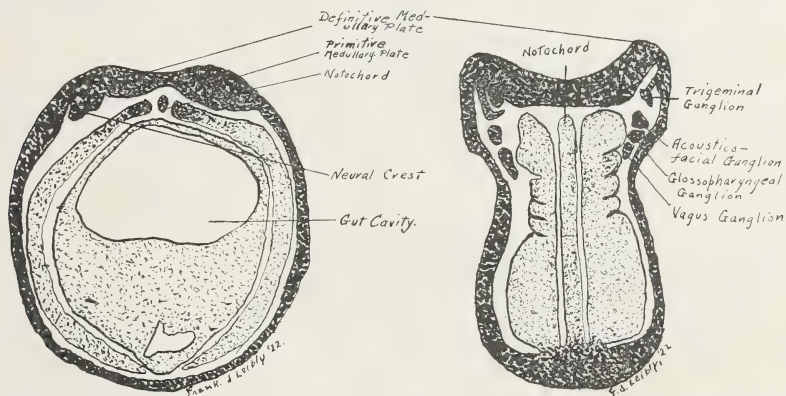


Fig. 334.

Transverse and frontal sections of frog embryo to show position and division of neural crest in head region.

The V, VII, IX, and X are called **branchiomer nerves** on account of their close relationship to the branchial clefts.

The cranial nerves take their substance from three embryological elements, namely: (1) the cell masses derived from the neural crests as described in the study of the chick, (2) cells from ectodermal patches on the surface of the head, and (3) from the cell processes which extend outward from the neuroblasts in the ventro-lateral walls of the spinal chord.

They differ, therefore, from the spinal nerves, for in these (2) is lacking.

The V, VII, IX and X cranial nerves arise by a single root (though this may be mixed, i. e., it may be both sensory and motor in function) to pass into a large ganglion. Beyond this ganglion a large horizontal branch is given off which in turn branches into **two rami** which pass anteriorly and posteriorly to the gill cleft with which the particular nerve is associated.

As in the chick, so in the frog, the cranial nerves develop from the **neural crests** left on each side of the central canal after the neural folds

fuse and the indented ectoderm again returns to its normal condition. The neural crests are thus left between the central canal and the outer ectoderm.

The neural crests are quite large in the head region, becoming smaller toward the posterior region of the embryo. Each crest becomes divided into three masses as the neural plate begins to close. (Fig. 334.)

The more anterior of these divisions, which lies in the region of the mid-brain, is the beginning of the V nerve; it forms the **trigeminal ganglion**. The middle section is the beginning of the VII and VIII

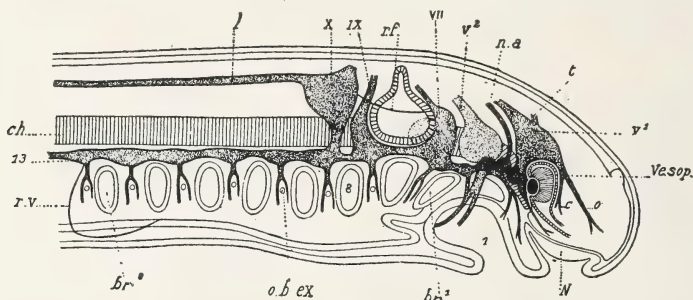


Fig. 335.

The Nerve Placodes in the head of an *Ammocoetes* 4 mm. long.  $V^1$ , first ganglion of the V cranial nerve;  $V^2$ , second ganglion of the same nerve; VII, ganglion of the VII cranial nerve; IX, ganglion of the IX nerve; X, ganglion of the X (Vagus) nerve, 1, 8, 13, first, eighth and thirteenth ganglia in the epi branchial series.  $br^1$ ,  $br^8$ , first and eighth branchial pouches; c, ciliary nerve; ch, notochord; l, lateral ramus of the X cranial nerve; N, anlage of hypophysis; n.a., VI cranial nerve (abducens); o., ophthalmic nerve; r.f., recurrent branch of VII cranial nerve (facial); r.v., recurrent branch of X (vagus) nerve; t., IV cranial (trochlear) nerve; ves.op., optic vesicle. (From Vialleton after von Kupffer.)

nerves; it is known as the **acustico-facialis ganglion**; while the posterior division forms the beginning of the IX and X nerves, or the **glossopharyngeal and vagus ganglia**. The three divisions do not separate entirely from the medullary plate, but remain connected by a very slender chain of cells to the medullary region of the brain.

When the tadpole has developed three or four somites, the inner or nervous layer of the ectoderm opposite the crest ganglia proliferates to form a patch, sometimes three or four cells in thickness. Such patches are known as **placodes** (Figs. 268, 335), and are thought to be **vestigial sense organs**.

In the placode there is found a **superficial sensory element**, which may disappear, and a **deep ganglionic element** which is usually retained. It is the ganglionic portion which fuses with the nearest crest-ganglion to form the principal sensory portions of the nerve.

### THE TRIGEMINAL OR V NERVE

This is the principal nerve of the mouth and mandibular arch. The trigeminal portion of the neural crest is large and extends from the eye to the hyomandibular cleft (Fig. 335). The ectodermal and mesodermal cell-groups fuse as the crest ganglion grows downward. In the ventral region it meets the mesoderm of the mandibular arch.

It is important that the student note how the **mesenchyme** of the mandibular arch is formed by the process of growth just described. The mesodermal and ectodermal cells have so intermingled at the point of fusion that the separate cells of ectoderm and mesoderm are now indistinguishable. (Fig. 334.)

The dorsal and superficial cells of the crest ganglion retain their nervous character and come into close relation to the large placode close to them; then the superficial sensory portion of the placode disappears. The deep or ganglionic portion not only enlarges, but divides into two parts. The anterior portion becomes the **ophthalmic ganglion** of the **ophthalmic branch** of the V nerve. The fibers of this branch grow cephalad through the dorsal head region, and also medially connect with the medulla oblongata.

The posterior portion of the placode ganglion fuses with the crest ganglion to form the **Gasserian ganglion** or **trigeminal ganglion**.

It is from the cells of the trigeminal ganglion that fibers arise which run to the medulla on the dorsal side. These fibers form the sensory root of the V nerve.

Then, too, there are fibers which grow out from the ganglion to pass to the surface of the head to form the **cutaneous branch** of the V nerve, while the fibers, which pass in front of and behind the mouth, are called the **mandibular** and **maxillary branches** respectively.

All of these branches, as well as those from most of the branchi-omeric nerves, can be seen before the opening of the mouth.

## THE FACIAL AND AUDITORY, OR THE VII AND VIII NERVES

Both of these nerves are derived from the acustico-facialis crest ganglion and the placode associated with it. The VII nerve is connected with the hyomandibular cleft, while the VIII nerve is a purely sensory (auditory) nerve, and so not one of the branchi-omeric series.

The greater portion of the crest ganglion, as with the V nerve, contributes to the mesenchyme of the hyoid arch, although the nervous portion of the crest ganglion is more extensive than that of the V nerve, which is due to the fact that a greater portion of the original ganglion retains its nervous function.

The superficial, or nervous, character of the placode does not disappear in this case, but keeps on becoming larger, after which it sinks below the surface of the head and invaginates to form the **auditory sac**. (Fig. 334.)

The deep placode ganglion cells which are in connection with this sensory epithelium remain in contact with the sac to form the **root** of the VIII nerve.

The remaining portion of the placode ganglion joins with the nervous portion of the crest ganglion to form the ganglion of the VII nerve. It is from this ganglion that fibers pass to the medulla and to the hyoid

arch and associated regions, to form the hyomandibular and palatine nerves.

### THE GLOSSOPHARYNGEAL AND VAGUS (PNEUMOGASTRIC) OR IX AND X NERVES

The remaining visceral clefts, that is, the first to fourth clefts, or third to sixth visceral arches, are associated with the IX and X nerves.

The IX nerve is limited to the first gill cleft alone, but the X nerve is associated and distributed to the others. It is to be considered a compound nerve, as it is made up of several branchiomic nerves.

The large posterior part of the neural crest in the head region is the portion associated with the IX and X nerves.

Its growth is much like that of the V nerve, though it does not assist in forming so much mesenchyme.

The superficial sensory portion of the placode of the IX nerve disappears, and its ganglionic portion is only slightly related to the crest ganglion.

Posterior to this, the larger placode of the X nerve appears simultaneously, and passes through similar stages; but in this case there is a more extensive fusion between it and the nervous portion of the crest ganglion.

The fibers from the IX and X ganglion pass out together to the medulla as a **single root**. The anterior cardinal vein partially separates the IX and X ganglion.

The fibers which pass out from the IX nerve portion of the ganglion are practically all placodal in origin, and pass to the first branchial cleft; while the fibers coming from the mixed ganglion of the X nerve are connected with all the remaining clefts.

It is well to pay considerable attention to the X nerve, as it is one of the most important nerves in the body, and is connected with many important structures.

It is from the X ganglion that other processes than those just mentioned, also grow. A considerable tongue of cells grows out posteriorly to form the sense organs of the **lateral line**, shortly to be discussed; while the fibers, which are to become the **lateral line nerves**, accompany this tongue (Fig. 340). These latter fibers are present only during the tadpole stage.

Then there are branches which pass to the thoracic and abdominal organs to form the visceral branch of the X nerve.

As sensory nerves pass to a general center, and motor nerves pass from a center to some outlying region, it is well to appreciate how some of the nerves mentioned above come to be **mixed**, that is, how they happen to have both sensory and motor fibers running along side by side.

The motor fibers of the branchiomic series do not arise by separate roots (Fig. 336) as do the sensory, but from neuroblasts in the

walls of the medulla oblongata which send out processes called **axons**, which leave the medulla in close association with the sensory roots already described. These are then distributed with the branches passing posterior to the gill clefts.

The III cranial nerve is the first of the remaining III, IV, and VI to appear, although all three of these form later than the ones discussed above, that is, they form when the tadpole is five to six millimeters in length.

The III is called the **oculo-motor**, the IV the **trochlear**, and the VI the **abducens**. All are motor nerves, which innervate the muscles of the eye-ball.

The I cranial nerve is the purely sensory **olfactory** nerve, and the II nerve is likewise a purely sensory nerve, namely, the **optic**.

### THE SPINAL NERVES

These nerves, unlike the cranial nerves, are related to the somites, and not to the visceral clefts, and no placodes are connected with them.

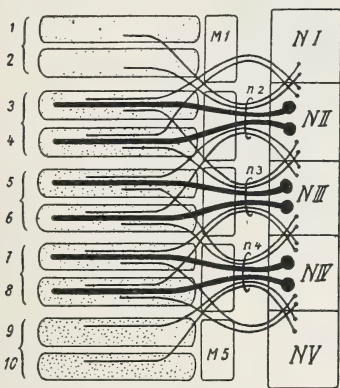


Fig. 336.

Schematic arrangement to show the composition of the central nerve roots in shark fins. The motor fibers run to the muscles, and each motor spinal root is made up of the fibers of three spinal segments. N1, N2, N3, N4, N5, Neuromeres; N2, N3, N4, corresponding motor roots; M1-M5, Myomeres; 1-10 Divisions of Myomeres. (From Rabl.)

The two most anterior myotomes do not have spinal nerves connected with them, and the myotomes soon disappear; but the segments formed in the neural crests, posterior to the head region (with the exception of the two just mentioned), have cell processes grow out into the cord to form the dorsal root of the spinal nerves, while others grow away from the cord to form the peripheral strands which are distributed to the skin and other sensory surfaces.

The ventral root of the spinal nerve is formed by outgrowths, or axons, from the neuroblasts on the ventral side of the cord, and appear when the tadpole is about four millimeters in length. These then meet the dorsal root a little distance beyond the ganglion, and pass partly to the mesodermal myotomes and partly to the sympathetic system.

### THE SYMPATHETIC SYSTEM (Fig. 337)

When the tadpole is about six millimeters in length, one may see a slight collection of cells on the spinal nerves at about the level of the dorsal aorta. From our study of the sympathetic system in higher animals, we assume that these cell-groups are composed of elements from the spinal ganglia, and from some of the posterior cranial ganglia.

The cells themselves migrate ventro-medially to form a pair of longitudinal **sympathetic cords**, along each side of the dorsal aorta. It is from these cords, then, that processes grow back to the spinal ganglia to form the **rami communicantes**, as well as outwardly to the various organs and surfaces.

Other fibers from other spinal ganglia grow out and follow the paths thus laid down for them, while cells from the sympathetic cord probably also migrate to form the large **sympathetic ganglia** found in close connection with the large blood vessels, and the thoracic and abdominal viscera. The fact of the matter is that the sympathetic nervous system

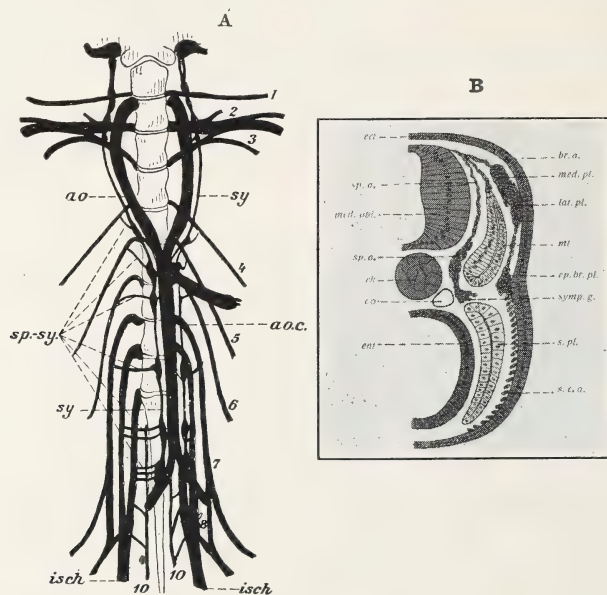


Fig. 337.

A. Sympathetic nervous system of the Frog. *ao*, aortic arch; *ao.c.*, common aorta; *isch*, ischial nerve; *sp.sy.*, communicating branches between the spinal and sympathetic nerves; *sy*, the two branches of the sympathetic system; 1-10, spinal nerves. (After Meissner.)

B. One-half of a transverse section of Ammocoetes, in the head-region. Schematic, *ao*, aorta; *br.a.*, branchial branch of nerves; *ch*, notochord; *ep.br.pl.*, ganglion anlage which develops where the epibranchial placode forms; *ect*, ectoderm; *ent.*, entoderm; *lat.pl.*, lateral placode; *med.pl.*, medial placode; *med.obl.*, medulla oblongata (hind-brain); *mt*, myotome; *s.c.a.*, subcutaneous branch of the epibranchial nerve placode; *sp.a.*, spinal branch running inward; *s.pl.*, lateral plate of mesoderm; *symp.g.*, sympathetic ganglion. (After von Kupffer.)

of the frog has not been worked out with any degree of thoroughness, and we can only suppose many things from our knowledge of other forms where more is known of this system.

The ganglion of the III cranial nerve is sympathetic in character, as other cranial nerves may be, but this must be left for future workers to demonstrate.

## THE EYE (Fig. 338)

The general method of the eye formation is quite similar to that already described in the case of the chick.

As the outer free rim of the optic cup draws together, it leaves a small opening which is the rudiment of the pupil. At this time we can distinguish the inner and outer layer to the cup, and a central cavity. These are the beginnings of the true **retinal layer**, the **pigment layer**, and the **posterior chamber** of the eye, respectively.

A choroid fissure is formed, just as in the chick.

The lens forms as a thickening of the ectoderm opposite the pupil, but this thickening involves only the nervous layer of the ectoderm. It develops quite like the ectodermal placodes in the formation of the cranial nerves. In fact, the lens placode lies immediately anterior to the placode of the V cranial nerve. About the time of hatching, the lens has formed a prominent rounded thickening entirely cut off from the ectoderm.

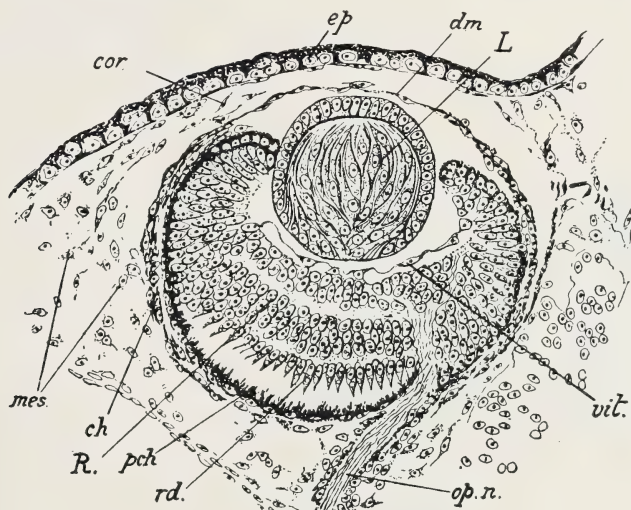


Fig. 338.

Section through the eye of a tadpole at the time when the operculum is forming, much magnified. *ch*, choroid; *cor*, mesoblast cells which will give rise to the cornea; *dm*, Descemet's membrane; *ep*, pigmented external epithelium; *L*, lens; *mes*, branched mesoblast cells; *op.n.*, optic nerve; *pch*, pigmented epithelium of the choroid; *R*, retina; *rd*, rods and cones pulled away from the pigmented epithelium of the choroid by contraction of the preparation; *vit.*, cells of the vitreous humour. (After Bourne.)

This spheroidal mass hollows out, although it again becomes solid by the cells on its inner side elongating, while the outer side remains as a thin epithelial layer covering the distal surface of the lens. Then, as the pupil narrows, the lens comes to lie just within the opening of the cup.

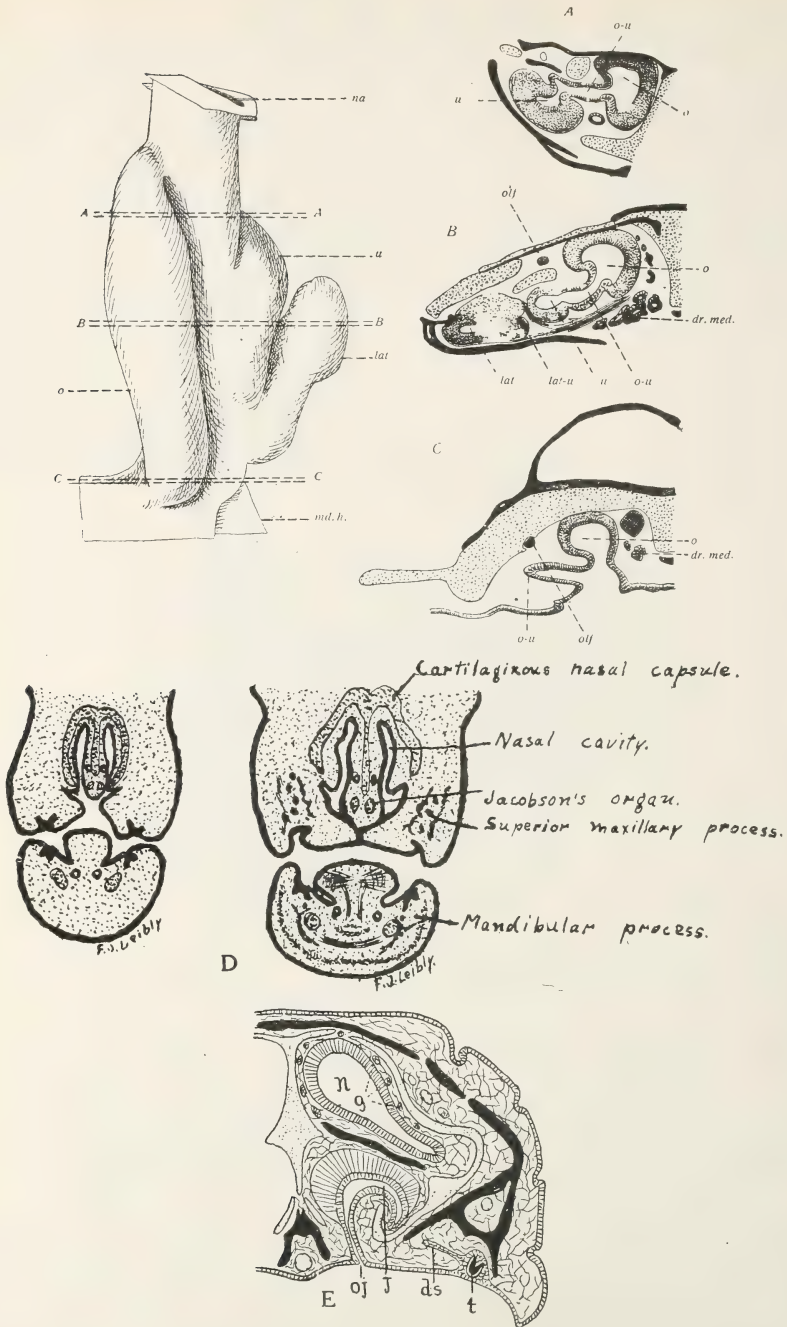


Fig. 339.

Reconstruction of smelling apparatus of Frog and three transverse sections (on the right) of tadpole through the regions marked *AA*, *BB*, and *CC*. *dr.med.*, glands on the medial side; *lat*, lateral view of the olfactory cavity; *lat-u*, com-

In the chick, and in fact in all vertebrates except the **Teleosts**, the lens forms as a hollow vesicle caused by the surface ectoderm invaginating. The choroid fissure of the optic cup closes a day or two before hatching. The closing begins opposite the pupil.

## THE EAR

The auditory placode appears just as the neural folds close. These placodes then become depressed below the surface of the head and invaginate to form the **auditory sac** or **otocyst**.

This sac at the time of hatching has become completely closed and separated from the ectoderm from which it arose. Therefore, it comes to lie in close relation to the lateral surface of the medulla.

The superficial layer of ectoderm continues to remain as a covering of the region where the placode invaginated. The wall of the auditory sac is but one cell in thickness, except in the medio-ventral region. It is in this region that the ganglionic part of the placode is located. There is a small finger-like outgrowth from the sac, which extends dorsally from the medio-dorsal region. This is to become the **endolymphatic duct**.

There is little change in the ear region from this time to the opening of the mouth, that is, until the tadpole is ten to twelve millimeters in length. Then development seems to begin again.

The remaining complicated changes in the formation of the inner divisions of the ear are beyond the scope of this book. The VIII cranial nerve connects with the ear.

## THE NOSE

The olfactory organs appear quite early, in fact before the brain closes (Fig. 339, *na*). A pair of ectodermal thickenings appears on each side of the head just above and anterior to the future mouth region. Again, only the deeper nervous layer is involved, as with the formation of the ear; only in this case, the superficial layer of ectoderm does not remain as a covering but disappears entirely. The thickenings themselves lie immediately anterior to the lens placodes, and are called **olfactory placodes**.

The placodes invaginate, forming the **olfactory pits** which are later to become the true nasal cavities (Fig. 339). A few cells from the inner surface of the olfactory placode become detached and come into communication with the surface of the fore-brain to form a sort of crest-

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munication of the lateral and lower region of the olfactory cavity; *md.h.*, wall of the mouth-cavity; *ma*, external nares; *o*, upper region of the olfactory cavity; *olf*, olfactory nerve; *o-u*, communication between the upper and lower regions of the nasal cavities; *u*, lower region of the nasal cavity. (After Bancroft.)

*D*, Frontal section of human fetus of 29 mm. (After Tourneaux.)

*E*, Sections through the nasal region. Bone black and cartilage dotted. *ds*, dent-shelf; *g*, Jacobson's glands; *j*, Jacobson's organ; *n*, main cavity of nose; *of*, opening of Jacobson's organ; *t*, tooth-germ. (After Schimkewitsch.)

ganglion. It is from these cells that the sheath cells of the true olfactory nerves (I cranial nerves) seem to be formed. The olfactory nerves themselves form from the sensory cells of the olfactory placode.

The **olfactory pits** are often said to form the **anterior nares**, while the openings from the anterior nares into the mouth cavity are called the **posterior nares**, **internal nares**, or **choanae**, all three terms meaning approximately the same thing.

The olfactory development is quite complicated and cannot be worked out in all details by the student in an elementary course such as this, but it is important that the main features be understood, so that light may be thrown upon later studies.

The epithelial lining of the olfactory pits forms a cavity on the dorsal side soon after hatching. This cavity then closes to form a separate dorso-lateral lobe, which disappears entirely as metamorphosis continues.

During metamorphosis, various thickenings and outpocketings appear in the olfactory organ, and there is a sharp bend in the main axis. The most important of the outgrowths is an extension from the ventral side of the olfactory chamber, where a solid mass of cells proliferates. This extended portion then acquires a cavity, grows rapidly, and turns transversely toward the medial side. This structure is to become Jacobson's organ (Fig. 339). A large glandular mass develops upon the medial end of this organ.

Opposite Jacobson's organ another growth appears which is non-nervous, that is, is not lined with nerve cells. This becomes a large sac, and the cavity of the sac is then added to the olfactory chamber. Still another growth appears anteriorly, close to the base of the olfactory duct. It is into this latter structure that the duct from the **lacrimal glands** enters. Still later (about the time of metamorphosis) a dorsal sac grows out from the medial and posterior walls of the tube.

During the late metamorphosis, the axis of the olfactory organ is sharply bent by the shifting of the internal nares, and other glands appear as outgrowths, both in the olfactory chamber and in the posterior walls of the internal nares.

## THE SENSE ORGANS OF THE LATERAL LINE (Fig. 340)

In all gill-bearing animals, and in all animals that have gills at any time during their development, such as the frog, a series of sensory organs develop, which are known as **lateral line organs**. These organs vary to a very considerable extent, but three or four of them are rather constant. These are: (1) the **supraorbital line**, which runs forward from the ear region over the eye to the tip of the snout. Twigs from the ophthalmic branch of the VII cranial nerve innervate it.

(2) The **infraorbital line**, which also runs from the ear region, but

passes **under the eye** to the snout. It is innervated by the **buccalis nerve** which is a branch of VII.

(3) The **hyomandibular line**, which runs along the jaw and operculum. This is innervated by twigs from the mandibularis externus and finally, (4) the **lateral line proper**, which may be double. This extends back to the tail on both sides of the animal, being innervated by twigs from the lateralis, a branch of the X cranial nerve.

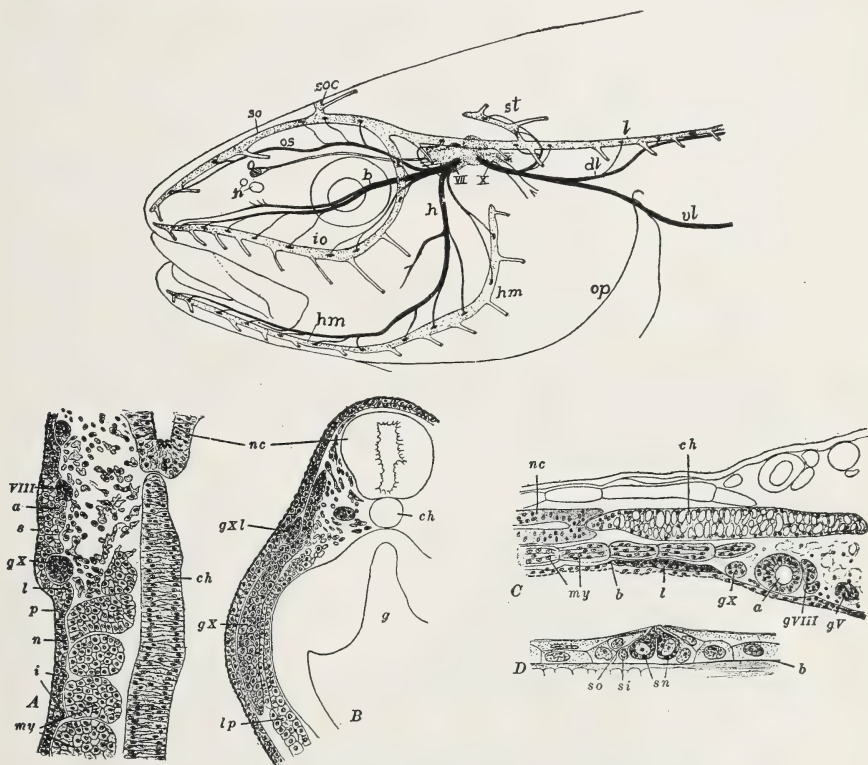


Fig. 340.

The development of the lateral line organs in *R. sylvatica*. *A*. Part of a frontal section through the level of the notochord of a 3.3 mm. embryo. *B*. Part of a transverse section through the vagus region of a 4 mm. embryo. *C*. Part of a frontal section through a 4 mm. embryo of *R. virescens*. *D*. Section through the lateral line organ of a 15.5 mm. larva of *R. sylvatica*. *a*, Auditory vesicle (in *A*, its rudiment); *b*, basemembrane of epidermis; *ch*, notochord; *g*, gut; *gV*, trigeminal ganglion, of V cranial nerve; *gVIII*, acoustic ganglion of VIII cranial nerve; *gX*, vagus ganglion; *gXI*, ganglion of the lateral nerve (branch of the vagus); *i*, intersegmental thickenings of the epidermis (ectoderm); *l*, rudiment of lateral line nerve; *lp*, lateral plate of mesoderm; *my*, myotomes; *n*, inner or nervous layer of epidermis (ectoderm); *nc*, nerve cord; *p*, pigment in epidermis; *si*, inner sheath cells of lateral line organ; *sn*, sensory cells of lateral line organ; *so*, outer sheath cells of lateral line organ. *E*, Lateral line canals and their nerves in a pollack (a fish belonging to the cod group). Canals and brain are dotted while the lateral nerves are black. *b*, buccalis ramus of the VII nerve; *dl*, dorsal ramus of lateralis of X nerve; *h*, hyomandibularis nerve; *hm*, hyomandibular line of organs; *io*, infraorbital line; *l*, lateral-line canal; *n*, nares; *o*, olfactory lobe; *op*, operculum; *os*, ophthalmicus superficialis nerve; *soc*, commissure which connects the lines of both sides; *so*, supraorbital line of organs; *st*, supratemporal part of lateral line *vl*, ventral ramus of lateralis of X nerve; *x*, visceralis portion of X nerve. (*A* to *D*, from Harrison; *E*, from Kingsley after Cole.)

There may be also a **supratemporal line**, connecting the systems of both sides and extending across the posterior portion of the skull from one side to the other.

These lateral line organs sink beneath the skin, and usually degenerate in water-forms of animals as soon as the animals are ready to live on land. In a few cases, such as **Tritons**, **Amblystoma**, etc., the organs are said to reappear when the animals return to water to deposit their eggs.

Various functions are assigned to these sensory line organs, but none has been clearly demonstrated. Probably they assist in recognizing differences in the vibrations of the water and may permit the animal to determine currents. They have been called a "sixth sense."

In the frog tadpole, the sense organs of the lateral line are derived from the placode of the X cranial nerve. The **ramus lateralis** of the X nerve innervates the organ.

When the embryo is about four millimeters in length, a small dorso-lateral section of the vagus ganglion is separated from (though lying close to) the ectodermal placode. The placode then begins to elongate posteriorly, while the deep cells proliferate rapidly to form a long, narrow tongue, which then pushes through the epidermis just outside the basement membrane. This tongue reaches as far back as the tip of the tail by the time of hatching.

Along this line, groups of cells form at intervals, each group representing the beginnings of a definite sense organ of the lateral line. In each group there are a few central sensory cells surrounded by a layer of enveloping cells. These groups then push up through the epidermis to the surface of the body, and the sensory cells develop hair-processes.

There are other tegumentary sense organs developing in definite rows on the head as well as dorsally from the mid-line to form those mentioned above, which are innervated by twigs from the VII, IX, and X cranial nerves.

All of the lateral line organs disappear, however, when the tadpole becomes an adult frog.

## CHAPTER XIII

### THE DIGESTIVE TRACT

**A**FTER the splitting of the mesoderm and notochord from the entoderm, the wall of the digestive tract is but one cell in thickness, except in the region of the mid-gut, where the yolk-mass is very large.

The stomodaeum, already discussed, is a shallow depression just below the olfactory and fore-brain region. This, by the time of hatching, while still very shallow, has its floor come to lie in contact with the wall of the fore-gut. The region in which these fuse is called the **oral plate** (Figs. 301, I, and 329, Pharyngeal membrane). It is at this point that the mouth forms a few days after hatching. The **oral sucker** (Fig. 337) forms just below the stomodaeal invagination.

The margins of the mouth form **mandibular ridges** which become drawn out as an upper and lower lip, the lower being the larger and freely movable. (Figs. 316, 317, 318.)

Strands of cells from the deep layer of the epidermis push toward the surfaces, and as each cell arrives at the surface it becomes cornified in a so-called "tooth." The upper lip has three rows of these "teeth," while the lower has four rows. All of these are lost when the tadpole assumes its adult shape. In the adult form, true teeth and jaws form.

From the fore-gut the following structures are derived (Figs. 328, 329, 337):

**The Pharyngeal Cavity**, the large expansion in the anterior portion of the fore-gut.

**The Oesophagus**, that portion of the fore-gut narrowed immediately dorsal to the yolk.

**The Visceral Pouches**, seen as vertical solid foldings extending to the surface ectoderm. Six pairs of these (compare this number with those found in the chick) develop, increasing in size and importance posteriorly.

**The Visceral Arches** (not to be confused with the pouches) are the vertical rods of mesoderm lying between the pouches.

**The hyomandibular pouch** is the name given the first pouch.

**The Mandibular arch** is the first arch, lying in front of the hyomandibular pouch, or in other words, between the hyomandibular pouch and the mouth.

**The I to V Branchial, or gill pouches**, are the remaining ones running posteriorly from the hyomandibular. The hyomandibular is the first in point of position, but bears a separate name. The numbers thus begin with the true second pouch.

The **Hyoid Arch** is the arch lying between the hyomandibular and I branchial pouches.

**Branchial Arches, or Gill Arches,** are the names given to the remaining arches.

The **Branchial Clefts, or Gill Clefts,** are the names given the various pouches after they have opened externally to the surface of the ectoderm, and internally into the pharynx. The second and third clefts are the earliest to become perforated, while the hyomandibular pouch does not become perforated at all, but disappears shortly after the first perforations occur.

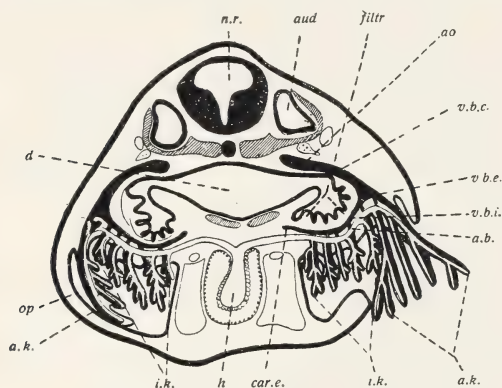


Fig. 341

Ideal diagrammatic transverse section through a 13 mm. frog tadpole, showing the first gill arch.

The right side shows the external gills (*a.k.*) extending through the gill opening which is almost closed. As the opening closes the gills draw inward. On the left side the gill opening is wide open with the external gills showing themselves free. *a.b.*, the first gill artery; *a.k.*, external gills; *ao.* aortic roots; *aud.* otic capsule; *c.e.*, external carotid; *d.* pharynx; *s.* lumen of the intestine; *filtr.* anlage of the filter apparatus (gill rakers); *h.* heart; *i.k.*, internal gills; *nr.* anlage of the neural canal; *op.* gill operculum; *v.b.c.*, common branchial vein; *v.b.e.*, external branchial vein; *v.b.i.*, internal branchial vein. (After Maurer.)

mouth opens. They become vascular and form the first breathing or respiratory organs of the tadpole. The posterior pair remain in a much more undeveloped state.

The **Operculum** (Fig. 341) is the name given to the covering of the external gills. It makes its appearance before the mouth opens, growing out from the posterior borders of the hyomandibular arches. These outgrowths extend backward so rapidly that by the time the anterior gills have reached their maximum size, the operculum covers them in what is called the **opercular cavity**.

The right opercular fold becomes fused with the body, while the left remains partly open to form the **opercular tube** or **spiracle**.

The **Internal Gills** form as tiny elevations on the postero-external faces of the branchial arches, just as the gill clefts are perforated. A thin layer of ectodermal cells covers them, just as it does the external

The **Eustachian tube** or **Tubo-tympanic cavity** of the ear, forms from the dorsal wall of the hyomandibular pouch.

The **External Gills** (Figs. 337, 341), which appear just before hatching, are small outgrowths from the outer surfaces of the dorsal ends of the first and second branchial (second and third visceral) arches. A small external gill also appears later on the third branchial arch. The two anterior gills grow rapidly and form large lobed processes by the time the

gills. These gill coverings become doubled on the first three branchial arches and remain a single row on the fourth branchial arch.

**The Gill Filaments** are the branched processes of the gills which become quite vascular and, as they project into the opercular cavity, permit the exchange of gases from the respiratory current of water entering the mouth, which current then passes through the gill clefts and the opercular tube.

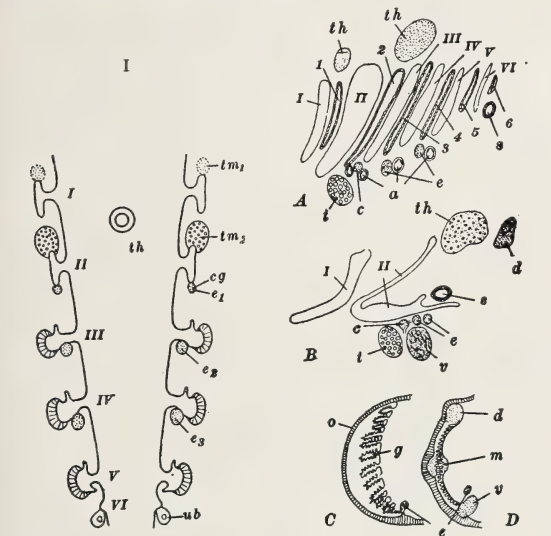


Fig. 342.

I. Diagram of the branchial pouch derivatives in the frog. (After Maurer, with Greil's modification.) *cg*, Carotid gland; *e<sub>1</sub>*, *e<sub>2</sub>*, *e<sub>3</sub>*, epithelioid bodies; *th*, thyroid body; *tm<sub>1</sub>*, *tm<sub>2</sub>*, thymus bodies; *ub*, ultimobranchial body; *I-VI*, first to sixth visceral pouches. (*I*, hyomandibular; *II-VI*, first to fifth branchial pouches.)

II. Diagrams of the derivatives of the visceral pouches and arches in the frog. *A*. Lateral view, frog larva. *B*. Lateral view, after metamorphosis. *C*. Transverse section through gill of frog larva. *D*. Transverse section through gill region, just after metamorphosis; the gills have not quite disappeared. *a*, Afferent branchial arteries; *c*, carotid gland; *d*, dorsal gill remainder; *e*, epithelioid bodies; *g*, internal gills; *m*, middle gill remainder; *o*, operculum; *s*, suprapericardial or postbranchial body; *t*, thyroid body; *th*, thymus bodies; *v*, ventral gill remainder; *I-VI*, visceral arches; *I*, mandibular arch; *II*, hyoid arch; *III-VI*, first to fourth branchial arches; 1-6, visceral pouches; 1, hyomandibular pouch; 2, hyobranchial pouch; 3-6, first to fourth branchial pouches. (Greil's Modification of Maurer.)

similar outgrowth from the hyomandibular pouch, but this disappears in a short time. The outgrowth which is to become the thymus grows slowly and separates entirely from the wall of the pouch when the tadpole is about twelve millimeters in length.

Both permanent and transient thymus bodies lie close to the outer surface of the head, immediately behind the auditory capsule and the articulation of the jaw.

**Epithelioid bodies** are similar to the thymus glands. These are

**The Velar Plates and Gill Rakers** (Fig. 341, *filtr*) form as tiny folds in the pharyngeal region which can be best understood by a study of the cuts. (The velar plates are the smooth inturnings of the floor of the pharynx while the jagged tooth-like foldings are the gill rakers.)

The structures mentioned above are practically lost when the frog reaches adulthood, although portions of these structures are used in building and forming other structures which will be discussed shortly.

**The thymus body** (Fig. 342) appears just prior to hatching. It is a solid internal proliferation from the epithelium of the upper side of the first branchial pouch (second visceral, or hyobranchial pouch). There is also a

formed from the **dorsal ends** of the other branchial clefts and become lymphoid in character.

**The Carotid Glands** form from the ventral ends of the **anterior gill pouches** as epithelial proliferations at about the time the internal gills appear.

**The Pseudothyroid Body** is a small outgrowth in the **postero-ventral branchial region**, apparently having no relation with the disappearing gill-clefts. This body disappears with the exception of traces of the middle and ventral portions which persist for a short time after metamorphosis, after which they, too, disappear.

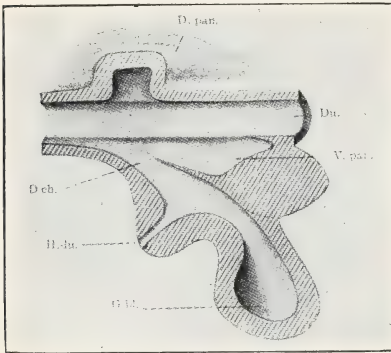


Fig. 343.

From a model of the duodenum and the primary evaginations of the liver and pancreas in a 5 mm. sheep embryo. *D.pan.*, Dorsal pancreas; *Du.*, duodenum; *D.ch.*, ductus choledochus; *G.bl.*, gall bladder; *H.du.*, hepatic duct. (After Stoss.)

**The Ultimobranchial Bodies** (also called post-branchial or supra-pericardial bodies) lie posterior to the fifth visceral pouch. They have formed as solid proliferations from the pharyngeal wall just behind the visceral (fifth) pouch, (fourth branchial pouch). These bodies are supposed to represent vestigial portions of a sixth pair of visceral pouches, although they do not extend to the surface ectoderm. They separate from the pharynx and acquire a lumen, coming to lie on the floor of the pharynx in a supra-pericardial position. (Fig. 342.)

**The Thyroid Body** is formed as a medial invagination from the floor of the pharynx just a short time before hatching. It forms as a solid rod of cells, but a few days after the opening of the mouth it forms a pair of bodies which grow rapidly and become very vascular. The thyroid body has no genetic relationship to the branchial structures nor do any of the following structures possess such relationship.

**The Lungs** develop just before hatching, as a pair of solid proliferations from the ventral wall of the posterior portion of the fore-gut, just between the yolk-mass and the heart. The cavities begin to form in the proximal region.

**The Laryngeal Chamber** (Fig. 332, B) is formed by the wall of the fore-gut between and around the lung diverticula which become depressed and form a groove, which then (at least partially) constricts off from the alimentary tract.

**The Glottis** is the opening which remains in the laryngeal chamber as it constricts.

**The Tongue** appears just before metamorphosis as an elevation in

the floor of the anterior portion of the pharynx, just behind the thyroid region. There is a glandular depression directly in front of the elevation which is carried forward by the anterior growth of the tongue, so that the glandular portion becomes the tip of the tongue.

**The Liver**, one of the earliest diverticula of the alimentary tract, appears even before the embryo itself has begun to elongate. It lies beneath the yolk mass and develops from the ventral portion of the fore-gut, just posterior to the heart. A group of scattered mesodermal cells lies between liver and heart, which will soon be added to the anterior wall of the liver rudiment. The anterior portion of the liver becomes folded after hatching.

**The Gall-bladder** is formed as a postero-ventral extension of the liver diverticulum which becomes more or less separated from the anterior portion of the liver.

**The Bile-duct** (Fig. 332) is the original opening of the liver diverticulum into the alimentary tract from which it grew.

**The Pancreas** (Figs. 343, 293) develops in close proximity to the liver diverticulum from three separate rudiments, a dorsal and two ventral. The dorsal rudiment is a solid outgrowth from the dorsal wall of the fore-gut. A complete separation between outgrowth and origin soon takes place.

The right and left ventral rudiments grow out of the fore-gut at the posterior margin of the bile-duct. These retain their connection with the gut, enlarge, and after passing around the bile-duct, fuse together in front of it. The dorsal portion later also fuses with this fused right and left portion and connects with the gut by the pancreatic duct. At this period, the pancreatic duct forms the boundary between the fore-gut and the mid-gut, although later the pancreatic duct comes to lie within the margin of the bile-duct. Oesophagus and stomach develop quite as they do in the chick. It will be remembered that the oesophagus closes for a time in the chick. It does likewise in the frog just after hatching, when the tadpole is about eight millimeters in length.

The oesophagus, however, again opens just before the mouth is formed, that is, when the tadpole is about ten or eleven millimeters long.

The stomach is at first longitudinal, but it soon bends, and comes to lie transversely. This position is a matter of importance when nerves are to be traced, for the nerves and blood vessels which are paired and known as right and left will now be dorsal and ventral, depending upon the side toward which the caudal end of the stomach turns.

## THE DERIVATIVES OF THE MID-GUT

As with the chick, the mid-gut is confined to that more or less central space where the yolk continues being absorbed and converted into other substances in the growing embryo and tadpole. After hatching,

the yolk is absorbed very rapidly, some of the yolk-cells becoming the epithelial lining of the growing intestine. The intestine is bent into a transverse loop, called the **duodenal loop**, with its proximal end at the posterior portion of the stomach. In fact, the intestine grows to almost nine times the length of the tadpole's body, but is shortened later to about one-third the body-length by the time metamorphosis takes place.

**The Hypochordal rod** is a structure which forms from the mid-gut as a medial ridge along the surface of its entodermal wall just underneath the notochord, although it has no relation to the notochord. It appears when the tadpole is three or four millimeters in length, and extends both cephalad and caudad, coming to lie free of the gut wall when the tadpole reaches a length of 4.6 millimeters. Finally, it can be seen as a caudal extension from the dorsal pancreas posterior through the tail. The rod itself is narrow, being only two or three cells in diameter. Just before the opening of the mouth, it breaks into pieces and disappears entirely.

### THE DERIVATIVES OF THE HIND-GUT

It is in this region that the neurenteric canal is found (Fig. 328), as well as the proctodaeum. The terminal end of the hind-gut, which is to become the rectum, fuses with the proctodaeum, and the anal opening perforates the thin sheet which has separated these two structures. This fusion and perforation takes place at about the time the tail begins to elongate, namely, when the embryo is about four millimeters in length. It is the proctodaeal region of both tadpole and frog which forms the **cloaca** into which rectal, excretory, and reproductive ducts enter. **The bladder** forms as a ventral outgrowth from the cloaca just before metamorphosis.

**The Post-Anal gut** is formed by the true hind-gut which remains within the embryo body proper as the tail continues growing. The nerve cord and notochord, however, are carried along in the growing tail so that the neurenteric canal is drawn out caudad. This neurenteric canal is then cut off from the nerve cord, but for a short period its antero-ventral portion opens into the rectum, and it is this which is known as the post-anal gut. This gradually closes, although a strand of cells can still be seen in the region at the time of hatching, extending nearly to the tip of the tail. It finally disappears altogether.

## CHAPTER XIV

### THE MESODERMAL SOMITES

**A**LL THE remaining systems to be described are intimately related to the mesoderm.

The mesodermal region in the chick, posterior to the head, divides into block-like segments by the formation of connective tissue septa which form at right angles to the long axis of the embryo. So, too, in the frog embryo and tadpole, the mesoderm divides into block-like segments. These are the **somites**. And, just as with the chick, so with the frog embryo, the mesoderm divides into an outer **somatopleure** and an inner **splanchnopleure layer** with an open space between them, known as the **myocoele**.

That portion of the somites which lie directly on each side of the notochord, is known as the **segmental, or vertebral, plate**, while the portion extending laterad from this segmental plate is called the **lateral plate**.

The lateral plates are, therefore, merely direct continuations of the segmental plates. However, as the somites divide off into blocks, the vertebral plates become thickened, and not only is the myocoele closed which lies within them, but a constriction along the long axis of the embryo separates the vertebral plate from the lateral plate.

As there are no somites in the head region, the mesoderm lies in the form of scattered groups of mesenchymal cells in the head and pharyngeal regions.

The somatopleure and splanchnopleure are not of equal thickness. The outer somatopleure is only one cell in thickness, while the inner splanchnopleure is much thicker. Therefore, the coelom which lies between these two layers, lies much closer to the outer portion of the embryo than to the inner portion.

The one cell-layer, which forms the outer somatopleure in the region where the somites have formed, is naturally segmented, as that layer is an actual portion of the somite proper. These one cell-layered segments of somatopleure are now called **dermatomes** or **cutis plates**, because they will soon join with the ectoderm lying immediately above them to form the outer wall of the embryo.

The segments of the splanchnopleure, which lie toward the center of the embryo, are called **myotomes**, or **muscle plates**, because it is from these that the muscle cells will form. In fact, the formation of the muscle fibrils can already be observed when the embryo is scarcely five millimeters in length.

It is the thickening of the myotomes which obliterates the myocoel quite early.

From the lower ends of each myotome, that is, from those regions lying ventral and close to the mid-line, cells proliferate and move downward beneath the notochord as well as upward between the notochord and the myotome. These proliferations form the **sclerotomes** which are to become the cartilaginous vertebral column.

Very early, that is, when the tadpole is only about five millimeters long, the somite proper separates from the lateral plates, and the sclerotomes separate from the lateral plates.

Immediately after this separation, there are ventro-lateral outgrowths from both myotomes and dermatomes. Those from the myotomes become the ventral musculature and extend into the limbs as voluntary muscles, while those from the dermatomes break up into groups of mesenchymal cells, some of which become connected with the inner surface of the ectoderm, and form the dorsal covering of the embryo, while some pass between the myotomes to form the connective tissue **septa**, also called **myocommata**. (Fig. 423.)

There are thirteen pairs of somites formed in the trunk of the frog, the two most anterior pairs disappearing in the adult. The full-fledged frog, therefore, has but eleven definite segments. The two anterior somites become part of the occipital region of the head. In the tadpole, there are many more somites than the amount stated above, but with the loss of the tail and the conversion of tadpole into frog, these are lost.

The following table will not only summarize the history of the somites and spinal nerves, but if carefully studied will show how the adult vertebral musculature which connects the posterior half of one vertebra with the anterior half of the next succeeding one, receives its innervation from more than one spinal nerve. A clear understanding of this will help the student very materially in his comparative anatomy. (See Fig. 336 also.)

#### TABLE OF SOMITES, VERTEBRAE, AND RELATED NERVES OF THE TADPOLE

(From Kellicott, after Elliot)

Cartilaginous Elements in Sclerotome	SOMITES		NERVES
	Embryo	Adult	Adult
Occipital Region of Skull	1	Absent (Disappears at formation of limbs)	Root of vagus nerve
	2	Absent (Disappears at formation of vertebrae)	No nerve. Ganglion in embryo only
	3	1	Ganglion and Nerve in embryo Absent in adult

1 Vertebra	4	2	1 Spinal Nerve (Hypoglossal)
2 Vertebra	5	3	2
3 Vertebra	6	4	Brachial Plexus
			3
4 Vertebra	7	5	4
5 Vertebra	8	6	5 to body wall
6 Vertebra	9	7	6
7 Vertebra	10	8	7
8 Vertebra	11	9	8 Sciatic plexus
9 Vertebra	12	10	9
Part of urostyle	13	11	10 to pelvic region

Even before the lateral plates are separated from the somites, there is a tendency to segment in the lateral plate itself, close to the somite. It is in this region that the excretory system is to be formed, and so these portions are called **nephrotomes**, or the **intermediate cell mass**. (Fig. 268.)

This mere trace of segmentation in the lateral plate lasts a very short time. In fact, the lateral plate itself never segments.

The cavity within the lateral plates is the true coelom. Just as in the chick, when the lateral plates extend further and further ventrally, they finally meet in the midline and fuse, to form a single coelom where there had been one on each side before.

This ventral fusion forms the **ventral mesentery** which soon disappears except in the heart region. The paired coelomic cavities also come together dorsally between the notochord and the digestive tract, and fuse to become the **dorsal mesentery**. This remains as a **suspensory arrangement** for the gut (Fig. 293). The gut itself later sinks more and more ventrally and the mesentery is pulled ventrad with it. The blood vessels supplying the digestive tract then grow downward through these two layers of mesentery.

# CHAPTER XV

## THE CIRCULATORY SYSTEM

### THE HEART

**I**MMEDIATELY cephalad to the liver, just ventral to the hinder part of the pharynx (Fig. 328), is the heart region. Here the somatic and splanchnic layers of mesoderm have separated by a wide cavity which is to become the pericardial cavity (Fig. 344), continuous for a time with the general body cavity, but later closed off.

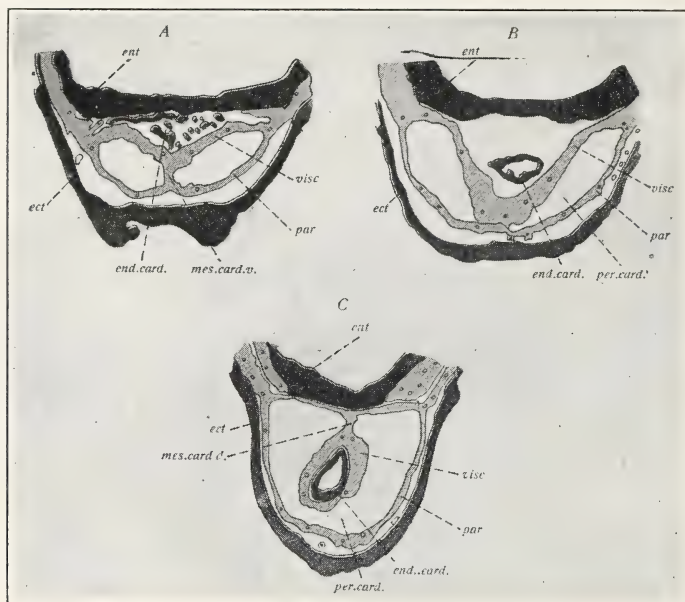


Fig. 344.

Cross sections of frog tadpole. *A* and *B* in the region of the anterior and posterior portions of the heart respectively; *C*, through a more or less mid-section of a more advanced tadpole, for comparative purposes. *ect*, ectoderm; *end.card.*, endocardium; *ent*, entoderm; *mes.card.d.* and *mes.card.v.*, dorsal and ventral mesocardium; *par*, somatic layer of mesoderm (somatopleure); *per.card.*, pericardial cavity; *visc*, visceral layer of mesoderm (splanchnopleure). (From Rudneff.)

Both pericardial wall and muscular wall of the heart are derived from the lateral plate mesoderm, **while the endothelium**—the inner lining of the heart—arises from scattered mesodermal cells lying between the splanchnic mesoderm and the digestive tract. These cells can be seen in the two somite stage.

From Figure 344 one can get a good understanding of how the

lateral plates extend beneath the pharynx and fuse in the midline to form the **ventral mesocardium**.

The splanchnic layer of the pericardium becomes folded dorsally so as to enclose the endothelial cells which have formed a more or less short tubular arrangement. Then the folds meet and fuse dorsally to form another tube on the outside of the endothelial tube. These latter tubes thus enclose the endothelial tubes and are connected with the dorsal wall of the pericardial cavity. The connection forms the dorsal **mesocardium**. The outer tube forms the muscle of the heart walls.

Much difficulty will be avoided in later studies if, after a review of the chick's circulatory system, the following account of the heart be mastered:

The paired endothelial tubes fuse together cephalad to form the **bulbus aortae**. Then there are outgrowths which form the beginnings of the **truncus arteriosus** or **ventral aortae**. The endothelial tubes do not fuse entirely in the posterior region, and are not alike on each side. The right one is bent and forms the beginnings of the **ventricle** and the **right vitelline vein**. The left one is slightly longer and larger in diameter in the more caudal portion. This is to become the **auricle**, while its continuation in a caudal direction will become the left **vitelline vein**. Both vitelline veins are connected directly with the yolk-mass and the liver.

As the embryo develops, the two endothelial tubes fuse quite like the letter S, after which the dorsal mesocardium disappears, so that, as in the chick, the heart tube is attached only at its two ends.

The heart now comes to have its caudal end toward the left side and resting against the liver. This caudal portion is the region of the **sinus venosus** and the **auricles**.

However, as the heart continues growing much more rapidly than the surrounding portions, and as it is attached only at its two ends, the cephalic region of the heart and the ventricle region swing downward and come to lie ventral in position. This naturally forces the auricle dorsad, and the auricle thus comes to occupy the greater portion of the dorsal side of the adult heart.

Constrictions separate the heart early into two limbs, but it is only after the tadpole's mouth has opened that the auricle is divided into right and left halves by the **inter-auricular septum** which grows ventrad from the dorsal wall. The sinus venosus remains connected with the right auricle, while the pulmonary veins later enter the left auricle. The pulmonary veins can hardly be seen during the tadpole stage.

The ventricle walls thicken, and a few days after the mouth opens, the bulbus aortae divide into an anterior and a posterior portion. The anterior portion is called the **truncus arteriosus**. This truncus arteriosus is also divided into right and left channels.

## THE ARTERIAL SYSTEM (Fig. 345)

The **Lateral Dorsal Aortae**, which are the first to appear, are paired and lie dorsal to the pharynx. They are formed from a series of separate spaces in the mesenchyme of the head region which then connect to form the vessels of the cranial region.

The **Dorsal Aorta** (Fig. 345, *ao*) is the name given the lateral dorsal aortae as soon as they fuse medially on the dorsal side of the embryo to form a single vessel. This vessel extends to the caudal extremity of the embryo.

The **Aortic Arch**. An aortic arch forms in each branchial arch, first as a little vascular space when the embryo is about 4.5 millimeters long.

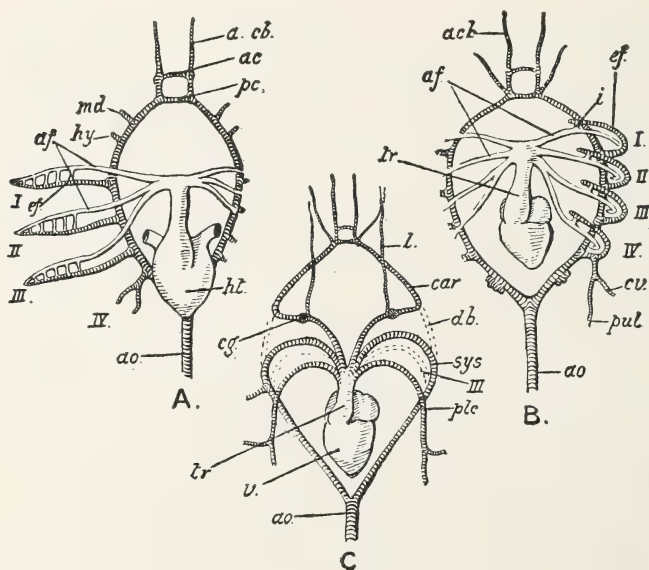


Fig. 345.

Diagrams of the heart and chief arteries of a tadpole. *A*, the vessels of a tadpole at the stage when three external gills are present; *B*, the arrangement when secondary gills are in use; *C*, the adult arrangement. *a.c.*, Anterior commissural vessel; *a.c.b.*, anterior cerebral artery; *af*, carotid gland; *cu*, cutaneous artery; *d.b.*, ductus Botalli; *ef*, efferent branchial arteries; *ht*, heart; *hy*, efferent hyoidean artery; *i*, connecting vessel; *l*, lingual artery; *md*, efferent mandibular artery; *p.c.*, posterior commissural vessel; *pl.c.*, pulmocutaneous arch; *pul*, pulmonary artery; *sys*, systemic arch; *tr*, truncus arteriosus; *v*, ventricle; *I-IV*, branchial aortic arches. (After Bourne.)

This space connects ventrally with the truncus arteriosus and dorsally with the lateral dorsal aorta (Fig. 341, *a.b.*). It is now called an **aortic arch**. There are **four pairs** of aortic arches lying in the third to sixth pair of gill arches. The first and second aortic arches are formed in the mandibular and hyoid arches.

The **Afferent Branchial Arteries** (Fig. 345, *af*). As the external

gills develop, a vessel forms dorso-laterally to the aortic arch, along the base of the gill to supply it. The vessel opens out of the ventral end of the aortic arch only to join it again at its upper end. The lower end of the aortic arch is then called the afferent branchial artery.

**The Efferent Branchial Arteries** (Fig. 345, ef). These are but the dorsal ends of the aortic arches. Loops of tiny capillaries form in the external gill to connect afferent and efferent vessels. Later, after the external gills are lost and the internal ones developed, part of the aortic arches disappear, so that afferent and efferent vessels are connected by vessels of the internal gills. This causes the original aortic arch to become almost entirely an efferent branchial artery, while the vessel which connected ventral and dorsal ends of the aortic arch becomes the afferent branchial artery (Fig. 345).

As the internal gills disappear when the tadpole becomes a frog, the lower end of the efferent branchial artery, which is the original aortic arch, again acquires a direct connection with the afferent branchial artery so that the blood again passes from truncus **arteriosus** to dorsal aorta.

The gill capillaries diminish and the connection, which has thus been re-acquired, becomes larger and forms the adult persistent vessels of the branchial arches. As the fourth branchial arch has no external gills developed upon it, the part described above regarding external gills does not apply to it. In all other respects, its blood supply is similar to those which do have external gills.

The above description applies to **Rana esculenta**, which, although different in detail, is essentially alike in all species.

The following account of the mandibular and hyoid vascular arrangement is for **Rana temporaria**:

**Hyoidean Vein.** This is a small outgrowth of the lateral dorsal aorta which extends toward, but never reaches the vessel which represents the aortic arch of the hyoid arch. It disappears at the time the mouth opens.

At the time of hatching, there is a small outgrowth from the truncus arteriosus extending into the lower end of the hyoid arch, but this, too, disappears shortly, though it is at this time that the vestige of the aortic arch has already become divided into dorsal and ventral portions. The dorsal portion also disappears, and the ventral becomes the hyoidean vein. This disappears with the oral sucker.

**Pharyngeal Artery.** Just before hatching, the vessels of the mandibular arch appear. Here, too, there is a vestigeal aortic arch in the lower portion of the mandibular arch, which soon unites with an outgrowth from the lateral dorsal aorta. After union, this vessel joins the hyoidal vein.

After the mouth opens, the outgrowth from the lateral dorsal aorta separates from the other vessels, growing forward. It is then known

as the **pharyngeal artery**, while, as mentioned above, the hyoidean vein disappears with the oral sucker.

**Anterior, or Internal Carotid, Arteries** (Fig. 345, car). These are the extensions of the lateral dorsal aortae into the head.

**Commissural arteries** (Fig. 345, ac). These are the two transverse connections between the internal carotids, which pass anterior and posterior to the infundibulum.

**Lingual, or External Carotid, Arteries** (Fig. 345, l.). These appear before the time of the mouth opening as a pair of sinuses in the buccal cavity. As the mouth opens, they extend backward to connect with the ventral ends of the efferent branchial arteries of the first branchial arch at the point where the carotid gland is to develop.

**Changes in Aortic Arches.** As soon as the gills disappear, there must naturally be a great modification in the branchial aortic arches (Fig. 345).

**Carotid Arch.** As already stated, a continuous aortic arch is reestablished in each of the four branchial arches when the afferent and efferent arteries fuse. The first branchial aortic arch, which is the third arch of the entire series, remains as the **carotid arch**.

**Systemic Arch.** The lateral dorsal aorta between the carotid arch and the aortic arch immediately posterior to it, is reduced to a solid strand of connective tissue and no longer functions, so that the second pair of aortic arches (the fourth of the whole series) form the roots of the dorsal aorta and is called the **systemic arch**.

**Pulmocutaneous Arch.** The third aortic arch (the fifth of the whole series) also becomes a solid strand of tissue and then disappears entirely, while the fourth (the sixth of the whole series) becomes the **pulmocutaneous arch**.

**Pulmonary Arteries.** These appear just after hatching as small outgrowths from the upper ends of the efferent branchial arteries of the fourth branchial arch, which then extend backward to the lung rudiments.

**Cutaneous Arteries.** These leave the pulmonary arteries and extend dorsally to spread out over the skin of both sides and back.

**Ductus Botalli.** This, it will be remembered, from our study of the chick, is that part of the fourth aortic arch between the lateral dorsal aorta and the origin of the pulmonary arteries (Fig. 345). This portion slowly atrophies and also becomes a solid strand. Three channels are now formed in the truncus arteriosus by various septa which divide it longitudinally. The carotid arches lead from one of these channels, which receives blood from the left side, while another carries venous blood from the right side of the heart to the pulmocutaneous arches. The remaining one connects the systemic arches.

## ORIGIN OF THE CIRCULATORY SYSTEM AND THE BLOOD

About the time of hatching, outgrowths of the dorsal aorta, just back of the pharyngeal region, extend laterally into the region of the pronephros or head kidney. These later become very large and form the vascular glomi of the kidney, traces of which remain long after the pronephros itself has disappeared.

In the frog the origin of the blood itself is by no means well established. The student should review the work on the chick in this respect. All we can say in regard to the frog is that when the embryo is almost ready for hatching, that is, when it is four to 4.5 millimeters in length, irregular spaces appear in the mesenchyme and splanchnic mesoderm, which later form continuous vessels. The corpuscles may arise as outgrowths from the endothelial lining of the blood vessels themselves, or from **blood-islands** which form on the ventral side of the yolk mass, or they may possibly form from both these sources.

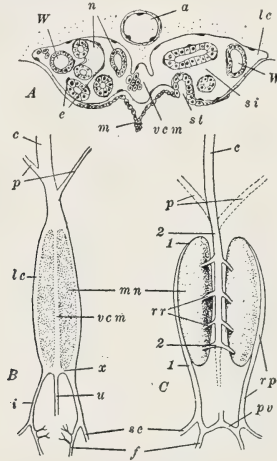


Fig. 346.

The development of the posterior part of the venous system in the frog. *A.* Portion of a transverse section through the posterior mesonephric region of an 18 mm. tadpole. *B.* Diagram of the veins of a 25-30 mm. tadpole. *C.* Diagram of the veins of the adult from. *a*, Dorsal aorta; *c*, vena cava; *e*, nuclei of the endothelial lining of the mesonephric sinus, continuous with the vascular endothelium; *f*, femoral vein; *i*, iliac vein; *lc*, lateral mesonephric channel of the posterior cardinal vein; *m*, mesentery, *mn*, mesonephros; *n*, mesonephric tubules; *p*, posterior cardinal veins (in *C* showing their original location); *pv*, pelvic vein; *rp*, renal-portal vein; *rr*, revehent renal veins; *sc*, sciatic vein; *st*, nephrostome; *u*, caudal vein; *vcm*, median mesonephric channel of the posterior cardinal vein; *W*, Wolffian duct; *x*, connection between caudal vein and the lateral mesonephric channels; 1-1, part of the renal-portal vein formed from the lateral channel of the posterior cardinal; 2-2, part of the renal-portal vein formed from the median channels of the posterior cardinal vein. (After Shore.)

## THE VENOUS SYSTEM (Figs. 308, 346)

**Omphalomesenteric, Vitello-intestinal, or Vitelline Veins.** These veins are really the first part of the vascular system to form in the region of the blood-islands. They are paired but not alike on both sides.

They pass along the lateral surface of the yolk and liver, and enter the sinus venosus. In fact, the sinus venosus is really formed by a fusion of these vessels from each side.

**Ductus Cuvieri or Cuvierian Sinuses.** These are a pair of large veins which enter into the sinus venosus also and may even form part of that organ. They come from the body-wall opposite the sinus venosus.

**Hepatic Vein.** As the liver develops, the omphalomesenteric veins, which pass through that organ, break up into capillaries within the substance of the liver. Then the parts of both omphalomesenteric veins, which lie between the liver and the heart, fuse into a single hepatic vein.

**Hepatic Portal Vein.** The right omphalomesenteric vein disappears caudad to the liver, while the left partly remains as the root of the future hepatic portal vein. This vein will later receive branches from the digestive tract as well as from those organs which have arisen from the digestive tract.

**Anterior Cardinal Veins.** As the ducts of Cuvier pass dorsad to the dorsal body wall, they divide. One branch passes headward as the anterior cardinal vein.

**Superior Jugular Veins.** This is the name given the anterior cardinal veins as they pass forward into the head, where they drain the brain and the dorsal portions of the head.

**Inferior Jugular Veins.** These drain the mouth, sucker, and ventral surface of the head, and open into the roots of the duct of Cuvier just before these in turn enter the sinus venosus.

**Posterior Cardinal Veins.** These are the posterior or caudal portions of the divided ducts of Cuvier, and are primarily the drainage system of the body-wall and excretory system. They pass caudad along the medial side of the pronephric ducts and receive the veins from the body-wall known as the segmental veins. The posterior cardinal veins form large sinusoids in the region of the pronephros, but as the metanephros develops, all this is modified, so that at fifteen millimeters the caudal ends of the veins fuse to form the single **median cardinal vein**.

**Caudal Vein.** This begins at the tip of the tail and drains that region. It is unpaired, but upon reaching the body cavity, divides above the cloacal region, and then empties into the posterior cardinal veins.

**Posterior or Inferior Vena Cava, or Postcaval Vein.** This begins as a branching of the left omphalomesenteric vein lying dorsal to the liver. From here, the postcaval vein passes through the suspensory fold of the liver to the right posterior cardinal vein and connects with it just anterior to the point where the median cardinal vein begins. This vessel enlarges rapidly to become the largest blood vessel in the body. It passes through the liver to the sinus venosus. The hepatic vein then opens into it instead of into the sinus venosus as formerly.

**Anterior, Superior, or Precaval Veins.** The pronephric portions of

the postcaval veins degenerate as the pronephroi degenerate, and ultimately disappear entirely, even before metamorphosis is complete. These leave the ductus Cuvieri as the proximal portions of the anterior cardinal veins, and it is these remaining proximal portions which are called the anterior, superior, or precaval veins. All blood from the posterior parts of the body-wall and from the tail now passes directly to the heart through the median cardinal and postcaval veins.

**Iliac Veins.** The pronephroi are followed by the mesonephroi as in the chick, and an alteration in the relation of the median cardinal vein follows. On each side of the body the developing mesonephroi push into the median cardinal vein, so that this vein is divided into one median and two lateral parallel channels. The caudal vein empties into the median channel and finally disappears, and the iliac veins, which come from the hind-legs, open into the lateral channels. It is the iliac veins which become the chief vessels leading to the mesonephric region after the caudal vein disappears.

**Adult Venous System.** After an understanding of the formation and change which takes place in the venous system during the embryonic period, the adult system can be understood.

**Afferent or Advehent Mesonephric Veins, or Renal Portal Veins.** These are merely the iliac veins, together with the lateral channels of the median cardinal vein, with which they are continuous.

**Posterior Vertebral Veins.** These are the small veins from the posterior body wall which open into the renal portal vein.

**Renal Veins, or Revehent Mesonephric Veins.** These are the short connecting vessels which connect the vascular space in the mesonephroi with the median channel of the median cardinal vein, so that only this median channel remains as a posterior continuation of the postcaval vein.

**Lateral Veins.** A pair of these develop late in the ventral abdominal walls, and open into the sinus venosus. The lateral veins connect with the iliac veins posteriorly, then fuse medially.

**Anterior Abdominal Vein.** The anterior ends of the lateral veins lose their connection with the sinus venosus, while the anterior portion of the right lateral disappears entirely. The left lateral vein forms a new connection with the hepatic portal vein, and is then called the anterior abdominal vein.

**Pulmonary Veins.** These can be seen, when the tadpole is about six millimeters in length, as projections of the endothelium on the dorsal side of the sinus venosus. These projections form a tube, opening proximally into the left side of the auricle, which distally leaves the wall of the sinus venosus, and passes dorsally to the lung rudiments. This tube bifurcates at the base of the lungs, where each branch then passes along the medio-ventral side of the lung rudiment. After the lungs begin to function, the pulmonary veins empty into the left auricle.

## THE LYMPHATIC SYSTEM

By the time the tadpole is 6.5 millimeters in length, one may see a single pair of "**lymph hearts**" (Fig. 11, Vol. I). They are sac-like, and grow out of the **intersegmental veins**, usually from the fourth pair. That is, they are outgrowths from the veins which run between the fourth and fifth myotomes. These "lymph hearts" empty into the posterior cardinal veins at the more caudal end of the pronephros.

The "hearts" themselves lie between the peritoneum and the outer covering, and below the level of the myotomes. The endothelial lining of the "hearts" and the blood vessels is continuous.

The "beating" of the lymph hearts is due to a syncytial layer or network of striated muscle fibers immediately outside of the endothelium. The "beating" begins about the time the mouth opens.

A short time after hatching, that is, when the tadpole is about 7.5 to 8.0 millimeters in length, two lymphatic vessels develop from each heart. They are known as anterior and posterior lymph vessels. They follow the lateral nerve in direction, the anterior vessel extending into the head, and the posterior along the sides of the trunk. Valves guard the openings of the lymph vessels into the "hearts" as well as into the veins where they empty.

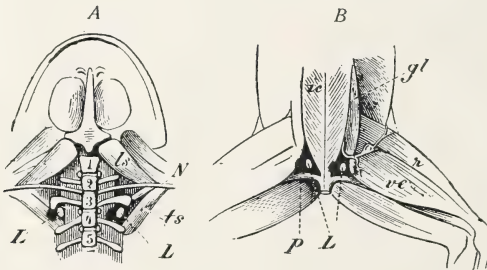


Fig. 347.

Frog. *A*, showing anterior lymph-hearts, from the dorsal side. *B*, showing posterior pair of lymph-hearts seen from the ventral side. *gl*, gluteus muscle; *ic*, iliooccygeal muscle; *L*, lymph-heart; *ls*, levator scapulae muscle; *N*, spinal nerve; *p*, piriformis muscle; *r*, vastus muscle; *ts*, transverse scapularis major muscle; *ve*, vastus externus muscle; 1-5, vertebrae. (After Wiedersheim.)

Immediately after these lymph vessels begin growing, they develop a rich network of capillaries which spread out in all directions. They are greatest in number close to the skin. Later, as the tadpole becomes quite large (about twenty-six millimeters), the lymphatic system becomes well developed.

The anterior lymph vessel, running downward and forward, connects with a large **lymph sinus**, around the mouth, heart, and branchial region. The posterior vessel passes caudad into the tail, and there divides into dorsal and ventral branches. These dorsal and ventral branches of each

side then unite to form two large vessels which extend through the tail, one of them above and the other below the myotomes.

The walls disappear in the network that has grown out from the lymphatic vessels to form the large subcutaneous **lymph sacs** already noticed in the dissection of the adult frog.

The **thoracic ducts** extend posteriorly from the "lymph hearts" and are probably outgrowths from them. They lie between the dorsal aorta and the posterior cardinal veins.

The **posterior lymph hearts** (Fig. 347)—(one to three pairs in number)—develop from the intersegmental vein just as did the anterior hearts, but their development is postponed until the hind-legs appear.

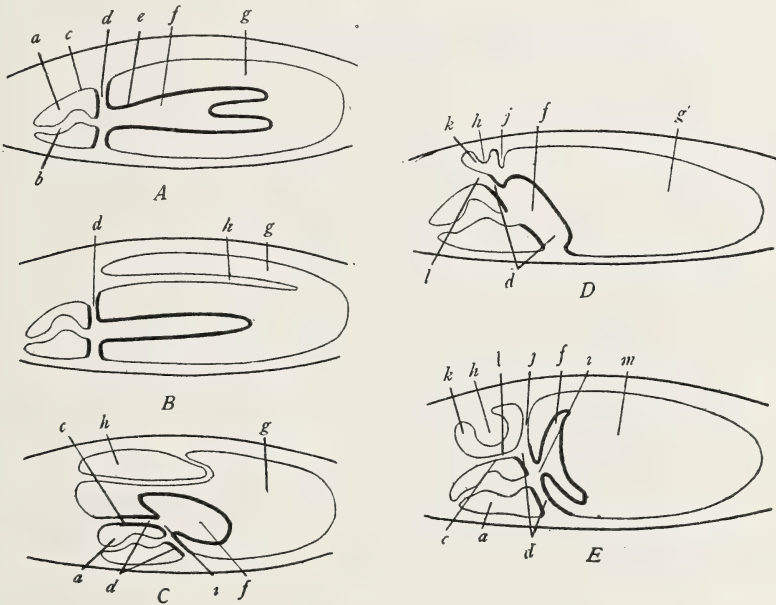


Fig. 348.

Diagrams to illustrate the divisions of the coelom in the various vertebrate classes. The transverse septum and its derivatives are indicated by thick lines. *A*, fishes, showing the division of the coelom into pericardial cavity *a*, and pleuro-peritoneal cavity *g*, by means of the transverse septum *d*. *B*, urodeles; similar to fishes with the addition of the lung *h* which projects into the pleuroperitoneal cavity *g*. *C*, turtle; the pericardial cavity *a* has descended posteriorly until it lies ventral to the anterior part of the pleuroperitoneal cavity *g*; the anterior face of the transverse septum, *d*, has now become part of the wall of the pericardial sac; the lung, *h*, is retroperitoneal. *D*, early stage of Mammals, showing the beginning of the coelomic fold (pleuroperitoneal membrane), *j*, descending from the dorsal body-wall, and the liver, *f*, enclosed within the transverse septum, *d*. *E*, later stage of mammals, showing union of the coelomic fold, *j*, with the transverse septum *d*, the two together forming the diaphragm which separates the pleural cavity *k* from the peritoneal cavity, *m*; the liver has constricted from the main part of the transverse septum, the constriction becoming the coronary ligament, *i*, *a*, pericardial cavity; *b*, heart; *c*, parietal pericardium or pericardial sac; *d*, transverse septum; *e*, serosa of the liver, this being a part of the transverse septum originally; *f*, liver; *g*, pleuroperitoneal cavity; *h*, lung; *i*, coronary ligament of the liver; *j*, coelomic fold which forms part of the diaphragm; *k*, pleural cavity; *l*, pleuropericardial membrane or anterior continuation of the transverse septum; *m*, peritoneal cavity. (From Hyman's "A Laboratory Manual for Comparative Vertebrate Anatomy," by permission of the Chicago University Press.)

Their first openings are into the posterior cardinal vein, which means that later they empty into the renal portal veins.

**The Spleen.** This ductless gland is first seen in the developing tadpole at about ten millimeters. It appears as a mass of mesenchymal lymphoid cells in the mesentery, immediately dorsal and posterior to the stomach and around the mesenteric artery.

These cells then multiply and project from the mesentery so as to have a peritoneal covering, as do all the organs in the body cavity. Later, as the spleen enlarges, various wandering cells from the intestinal epithelium seem to be added to it. The spleen is complete and extremely vascular by the time the tadpole is twenty-five to twenty-seven millimeters in length.

### THE SEPTUM TRANSVERSUM (Fig. 348)

The pericardial cavity, already discussed, has remained open posteriorly into the abdominal cavity, with the exception of the region covered by the liver. Now, as the ducts of Cuvier form and pass from the body-wall to the sinus venosus, they pass through this open region and carry with them incomplete peritoneal folds from the body-wall. These folds are called the **lateral mesocardia**. They remain incomplete dorsally for a long time, but gradually extend ventrally so as to form a complete separation between pericardial and peritoneal cavities. This transverse partition is called the **pericardio-peritoneal septum** or the **septum transversum**. To this septum transversum is added a medial portion of peritoneum from the anterior face of the liver, while on the right side the septum becomes continuous with the posterior suspensory fold of the liver commonly called the **mesohepaticum**.

After metamorphosis, the septum unites dorsally with the dorsal mesentery and completes the separation between pericardial and peritoneal cavities.

## CHAPTER XVI

### THE UROGENITAL SYSTEM

FROM our study of the urogenital system of the chick, we learned that while in birds and mammals, a pronephros, a mesonephros, and a metanephros form, in amphibians, the first two forms of nephridic organs alone make their appearance, the mesonephros then remaining as the permanent adult functioning kidney.

We have already spoken of the **nephrotomes**, which are also called the **intermediate cell mass** (Fig. 268).

Some time before hatching, when the embryo is only about three to four millimeters in length, this intermediate cell mass can be seen as longitudinal thickenings on each side of the notochord. These thickenings then form a groove, the lips of which soon fuse to form a tube or duct. This is the **pronephric** or **segmental duct**. It is at the anterior end of this pronephric duct (in the region of the second to fourth somites) that the pronephros or head-kidney forms as a ventro-lateral outgrowth.

At this anterior end of the pronephric duct three tiny openings are left as the lips of the duct fuse. These three openings become the three **pronephric tubules** (Figs. 349, 350), and the openings of these tubules into the coelom are called the **nephrostomes**.

The nephrostomes become lined with large cilia which produce a current out of the coelom. This current then passes by way of the pronephric duct to the cloaca.

The pronephros itself becomes quite vascular. In the discussion of the posterior cardinal veins, mention was made of the close relation of these veins to the excretory system. It will be remembered that they lie along the pronephric ducts. The elongating of the pronephric tubules pushes them upward into the posterior cardinal sinus until the sinus is nearly filled. This means, of course, that the tubules are really bathed in venous blood. At the same time that this occurs, arterial blood is brought from the dorsal aorta to the excretory system by arteries in the form of glomeruli.

The manner in which the glomeruli form is rather complicated. Opposite the second nephrostome, a fold appears in the splanchnic mesoderm, when the embryo is about 4.5 millimeters long. This fold lies parallel to the pronephros itself, becoming elevated and projecting into the coelom opposite the nephrostomes. Vascular spaces appear in this fold, which develop into long convoluted vessels of the glomerulus proper, and also into a definite vessel which connects with a branch from the dorsal aorta.

This region of the body cavity is later cut off from the **pronephric chamber** by the lungs, projecting laterally, and carrying a fold of peritoneum across to the peritoneum which covers the pronephros, fusing with it for a short distance. The pronephric chamber remains open into the coelom both anteriorly and posteriorly to the lung region.

The **pronephric capsule** is derived from two sources, namely: from the ventro-lateral walls of the myotomes, which normally give rise to mesenchyme but which here evaginate in the pronephric region over

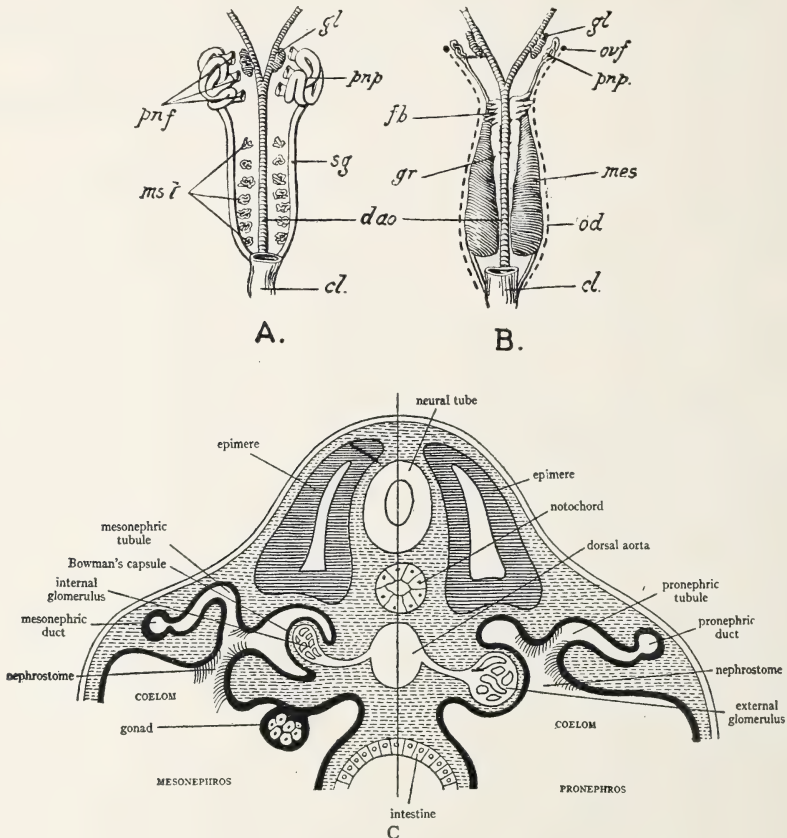


Fig. 349.

*A* and *B*. Diagrams of the development of the excretory system of the frog. *A*, The system of a tadpole about 12 mm. long, showing the pronephros and origin of the mesonephric tubules; *B*, the system at the end of the metamorphosis. The broken line represents approximately the position of the strip of peritoneal epithelium which gives rise to the oviduct. *cl.*, Cloaca; *d.a.o.*, dorsal aorta; *f.b.*, fat body; *gl.*, glomerulus; *gr.*, genital ridge; *mes.*, mesonephros; *ms.t.*, mesonephric tubules; *od.*, oviduct; *ovf.*, position of oviducal opening; *pnp.f.*, pronephric funnels; *pnp*, pronephros; *sg.*, segmental duct. (From Bourne.)

*C*, Diagram to show the structure of the pronephros and the mesonephros. Pronephros on the right and mesonephros on the left. The chief difference is in the relation of the glomerulus; in the pronephros it projects into the coelom; in the mesonephros it projects into the tubule, which forms the Bowman's capsule about it. (From Wiedersheim.)

both dorsal and lateral surfaces of the head-kidney to meet with folds coming up from the somatic layer of the lateral plate. This forms a capsule of connective tissue which encloses not only the pronephros proper, but also the pronephric sinus of the posterior cardinal vein.

The pronephros is largest when the tadpole is about twelve millimeters long. It remains stationary until the twenty millimeter stage, when it begins to degenerate. Degeneration is not quite complete at metamorphosis. Various blind outgrowths of the three original tubules can be seen before degeneration sets in. The pronephric duct closes just posterior to the pronephros and the tubules break up and disappear.

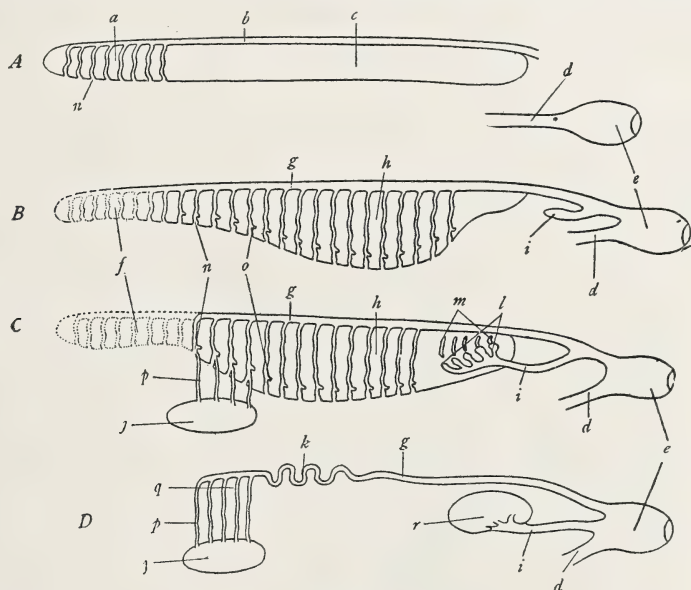


Fig. 350.

Diagrams to show the development of the three kidneys and their ducts and their relation to the male gonad. *A*, early stage showing the pronephros *a*, developing from the anterior end of the mesomere *c* and the pronephric duct *b*, which has not yet reached the cloaca *e*. *B*, next stage illustrating the degeneration of the pronephros at *f*, the development of the mesonephros *h*, from the middle portion of the mesomere, the junction of the pronephric duct, now the mesonephric duct *g* with the cloaca and the beginning of the metanephric evagination *i* from the mesonephric duct. *C*, later stage, showing connection between certain tubules of the mesonephros and the testis *j* by means of tubules, the vasa efferentia, *p*, which grow out from the mesonephros; and the penetration of the metanephric evagination into the posterior end of the mesomere where it is subdividing to form the collecting apparatus *l*, which becomes associated with the secretory metanephric tubules *m*, developed in the mesomere. *D*, final stage, in which the mesonephros has disappeared except for the remnant *q*, which connects with the testis *j* by means of the vasa efferentia *p*; the mesonephric duct *g* persists as the vas deferens; the two parts of the metanephros shown in *C* have united to form a single organ *r*. *a*, pronephros; *b*, pronephric duct; *c*, mesomere or nephrotome; *d*, intestine; *e*, cloaca; *f*, degenerating pronephros; *g*, mesonephric or Wolffian duct; *h*, mesonephros or Wolffian body; *i*, metanephric evagination from the Wolffian duct in *B*, ureter in *C* and *D*; *j*, testis; *k*, coiled portion of the vas deferens forming part of the epididymis; *l*, collecting part of the metanephros derived from the Wolffian duct; *m*, excretory tubules of the metanephros derived from the mesomere; *n*, nephrostome; *o*, renal corpuscle or Malpighian body; *p*, vasa efferentia; *q*, remnant of the mesonephros, forming part of the epididymis; *r*, metanephros. (From Hyman's "A Laboratory Manual for Comparative Vertebrate Anatomy," by permission of The Chicago University Press.)

The nephrostomes, however, approach one another, and finally meet to open into a common cavity, called the **common nephrostome**. This, then, also closes so that the nephrostomes are entirely cut off from all communication with the body cavity. The glomeruli also disappear, although traces of these can still be seen for some months after metamorphosis.

## THE MESONEPHROS OR WOLFFIAN BODY

Just about the time the pronephros attains its full size, or a little before, the mesonephros, or Wolffian body, begins to form in the region of the nephrotomes or intermediate cell-mass of the seventh to twelfth somites. It is both somatic and splanchnic in origin. These nephrotomes fuse in a continuous longitudinal strip of irregularly arranged cells which lie between the pronephric duct and the dorsal aorta, along the posterior cardinal vein. Little swellings appear in this mass, which are the beginnings of the **mesonephric vesicles**. They are more numerous than the mesodermal segments, and so are not strictly metameric.

Each of these swellings divides into a large ventral and a smaller dorsal chamber; the larger one is called the **primary mesonephric unit** and the smaller the **secondary mesonephric unit**.

The secondary units divide later to form a **tertiary mesonephric unit**.

Each of the three units develops much alike. Figures 349 and 350 show this development. There are two outgrowths, an **inner tubule** which grows dorso-laterally to the pronephric duct where it opens, and an **outer tubule** which grows ventro-medially to the peritoneum with which it fuses, and then it empties into the body cavity.

The inner tubules connecting with the mesonephric duct convert the portion where such connections are formed into the mesonephros or Wolffian body—the true kidney of the adult frog. The duct itself, in the region of the connections, is known as the **Mesonephric, or Wolffian, Duct**, while the duct posterior to this region is now the **ureter**.

The inner tubules become elongated and coiled to form the tubular portion of the mesonephros, while the outer tubules form outgrowths which later form the capsule around the glomeruli, known as **Bowman's capsules**.

A small twig from the dorsal aorta connects with each glomerulus in a similar manner to the way the glomeruli were formed in the pronephros. The proximal portion of the outer tubule, from which the outgrowths arise to form the capsule, now separates from the remaining tubule, but retains its connection with the inner tubule, and the distal portion of the outer tubule comes to lie in connection with the body cavity. This latter connection becomes ciliated and forms a typical

nephrostome as in the pronephros. The nephrostomal region now forms another connection at its inner end with the sinus of the posterior cardinal vein, in which sinus the mesonephric tubules lie surrounded by venous blood.

Many, as high as two hundred, outer tubules and nephrostomes may be formed from the three units described, and possibly some may be formed also by independent evaginations from the peritoneum, or even by splitting of those previously formed.

The **urinary bladder** is a median ventral outgrowth from the wall of the cloaca nearly opposite the openings of the ureters.

## THE REPRODUCTIVE SYSTEM

The mesonephric duct becomes divided somewhat obliquely into two portions in front of the mesonephros, the more anterior portion now being the Müllerian duct, while the posterior portion forms the Wolffian duct. The Müllerian duct connects with the peritoneal epithelium anteriorly and empties posteriorly into the cloaca. In the male frog, this duct persists as a mere longitudinal streak on the outer side of the kidney, and extends some distance in front of it. In the female frog, this Müllerian duct becomes the oviduct (Fig. 350).

The Wolffian duct functions as the ureter in both sexes, but in the male, the posterior end of it becomes dilated into a glandular enlargement, called the **seminal vesicle**.

Already at the six millimeter stage, as the mesentery is being formed by the coming together of the somites from both sides just under the dorsal aorta, a small group of entodermal cells is pinched off from the yolk, which, after completely separating from the yolk, divide longitudinally, each half moving laterally. These longitudinal halves are the **genital ridges** (Fig. 349, B). They lie close to the mesenteric attachment, and just beneath the cardinal veins.

The genital ridges become quite conspicuous in a short time by germ-cell proliferations as well as by the peritoneal cells which cover them and the mesenchymal cells from the body wall which migrate to this region.

The mesenchymal cells form the **stroma** of the ridge; the peritoneal cells form a thin superficial covering at first, while later they also form the suspending folds (**mesorchia** of the testes, and **mesovaria** of the ovaries) of the gonads. The germ-cells now begin to proliferate and form the **nests of cells** (Fig. 254) which are to develop into gonads and gametes as already described early in the embryology of the chick.

The anterior portion of the genital ridge becomes the **fat body** shortly before metamorphosis, while the posterior portion connects with the mesonephric duct.

In this posterior region several outgrowths from the Malpighian

bodies, known as **sexual cords**, can be seen. These become tubular, and extend into the substance of the gonad. In the male, these sexual cords, after metamorphosis, form the **vasa efferentia**, or **efferent ducts**, by which spermatozoa are carried from the gonad proper to the real sperm duct, the **vas deferens**. In the female, the portions between ovary and mesonephros degenerate, remaining only as a vestige, called **Bidder's organ** (Fig. 457).

The tadpole must be of considerable size before the sexes can be distinguished. Bouin gives the length as thirty millimeters in *Rana temporaria*. In the male gonad, the cells all look alike, while in the female gonad, the follicle arrangement can be made out, and the ovary acquires a central lumen.

### THE ADRENAL BODIES OR EPINEPHROI

Figure 351 will show how the adrenal bodies grow on the mesonephros of the frog. The important point to remember is that **there are**

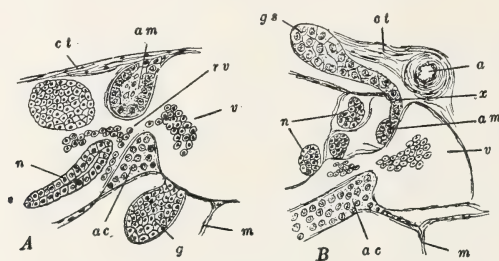


Fig. 351.

Parts of sections through young *R. temporaria*, showing the origin of the adrenal bodies. *A.* Through 30 mm. tadpole. *B.* Through 11 mm. frog after metamorphosis. *a*, Dorsal aorta; *ac*, cortical cells of adrenal body; *am*, medullary cells of adrenal body; *ct*, connective tissue; *g*, gonad; *gs*, sympathetic ganglion; *m*, mesentery; *n*, mesonephros; *rv*, efferent renal vein; *v*, vena cava; *x*, point where ganglion cells enter mesonephros and adrenal body. (After Srdinko.)

**two kinds of cellular substances in these organs.** The adrenal bodies lie on the ventral surface of the mesonephros in the frog.

Histologically, one may see a coarse network of cell strands with occasional groups of darkly staining tissue, called **phaeochrome tissue**. Blood from the median posterior cardinal vein occupies the spaces in the adrenal body. The coarse network forms what is called the **cortical tissue**, while the more darkly staining portions are known as **medullary tissue**, because in the higher forms of animal life, the darkly staining portion lies toward the inner region of the organ, and the coarse network lies toward the outer or cortical region.

When the tadpole is about twelve millimeters in length, the cortical

region appears as small groups of cells lying along both sides of the wall of the median posterior vein, below the level of the mesonephros, as well as beneath the peritoneal epithelium from which they seem to arise.

Just after metamorphosis, these cell-groups separate from the peritoneum to form the network mentioned.

The medullary portion, however, has a totally different origin, and one which may throw light on further work in the study of ductless glands, whose secretions have become an important factor in modern medicine. This portion is derived **from the ganglia of the sympathetic nervous system** by groups of cells whose precise origin is not clear. Some of these cell groups remain in the sympathetic ganglia, but others migrate to the adrenal body and become scattered about.

## CHAPTER XVII

### THE SKELETAL SYSTEM

**T**HE notochord extends from the blastopore to the pituitary body, as a rod of vacuolated cells filled with fluid, around which three layers or sheaths form.

The **primary** or **elastic sheath**, is an outgrowth of superficial cells of the notochord itself and forms the superficial surface sheath of the notochord.

The **secondary** or **fibrous sheath** is formed between the primary sheath and the notochord also by cells from the notochord itself.

The third or **skeletogenous** sheath forms on the outside of the primary layer at a later period as a thin sheath which is formed by the **sclerotomes**. The sclerotomes, it will be remembered, are outgrowths from the somites. This skeletogenous layer extends dorsally, entirely around the neural tube, and laterally, from the notochord, in between the successive myotomes. It is in this skeletogenous layer that the vertebrae are to be formed.

When the tadpole is about fifteen millimeters long, a series of metameric cartilages can be observed along the medio-ventral surface of the notochord. They lie in the skeletogenous sheath (Fig. 352, cs). These segments fuse longitudinally to form a pair of dorsal and ventral strips which extend along the entire notochord.

These strips now become metameric by constrictions of fibrous tissue which form rings. The rings are the beginnings of the **inter-vertebral ligaments**, which, just as in the chick, appear opposite the middle of each mesodermal segment.

The mesodermal segments become the vertebrae, so that the ligaments which form as separate segments between the vertebrae, are able to act on both the vertebrae lying immediately anterior and immediately posterior to each mesodermal segment, after the muscle has developed in connection with these ligaments (Figs. 305, 352).

The notochord becomes segmented and surrounded by cartilage, the notochordal segments form the soft centrum of the vertebrae, and probably also portions of the intervertebral discs.

The ventral cartilages now grow around the sides of the notochord and meet to fuse with the dorsal series.

The **transverse processes** of the vertebrae grow out from the ventral cartilages. It is toward the lateral ends of these that the transverse processes of the ribs later develop.

The **neural arch** is formed from outgrowths of the dorsal series which grow inward beneath the neural cord and also dorsally and ven-

trally. Later, when ossification begins, short processes called **inter-vertebral articulatory processes** develop from the neural arches, by which each vertebra joins with the next succeeding vertebra.

Ossification begins in the tadpole between the dorsal and ventral series of cartilages, just described. There are nine vertebrae formed in the frog, plus the urostyle, the latter being unsegmented.

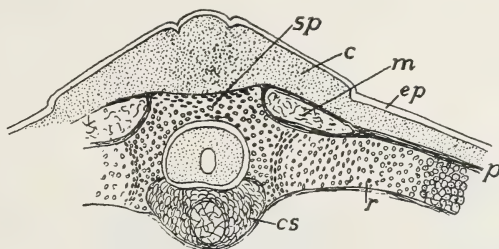


Fig. 352.

Cross section through a developing vertebra, rib and exoskeleton of a Turtle. *c*, corium in which the dermal plates are developed; *cs*, primitive vertebral body; *ep*, epidermis; *m*, external oblique muscle; *p*, perichondrium; *r*, rib; *sp*, spinous process. (From Kingsley after Götte.)

## THE SKULL

The skull is commonly formed from various embryological elements, which may be listed as follows:

- (1) Cranium.
- (2) Sense Capsules.
- (3) Visceral Arches.
- (4) Notochord.
- (5) Vertebrae.
- (6) Membrane or Derm Bones.

It will be remembered that there are no true segments in the head region of the frog. Consequently, the list just given is only **assumed from a comparison of other forms**.

When the cranial region begins its cartilage formation, the tadpole is about seven millimeters in length. A pair of dense strands of tissue form along the ventro-lateral surfaces of the fore-brain. These then become cartilaginous and form the beginnings of the **trabeculae** or **trabecular cartilages** (Fig. 310). These trabeculae extend forward and fuse across the midline between the olfactory organs. The fusion forms the **internasal plate**. The trabeculae continue extending forward, and these extensions are known as the **trabecular cornua**, at the ends of which the **olfactory capsules** form.

A pair of **labial** or **supraostrail cartilages**, which have formed in the upper lip, meet with the olfactory capsules.

The notochord, which extends into the brain up to the pituitary body, has a pair of tissue thickenings beginning in the region of the

hind-brain and extending anteriorly as **parachordae**, or **parachordal cartilages**. These parachordal cartilages now fuse with the posterior ends of the trabeculae to enclose the tip of the notochord, and the entire continuous plate beneath the fore-brain is then called the **parachordal plate**.

These parts can be made understandable only by a careful examination of Figures 310 and 353, which must be studied with great thoroughness or much of the later work in comparative anatomy will be valueless.

From the visceral arches, the **palato-quadrates** are formed as a pair of flattened rods, lateral to the trabeculae. These are in intimate rela-

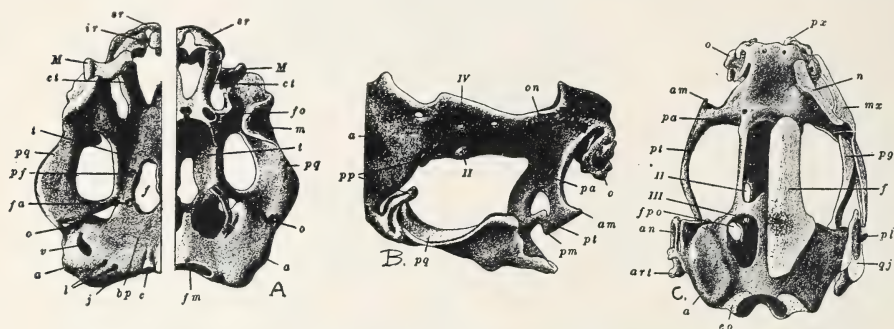


Fig. 353.

**A.** Chondrocranium of 29 mm. larva of *R. fusca*. To the left, the ventral surface; to the right, the dorsal surface. *a*, Auditory capsule; *bp*, basal plate; *c*, notochord; *ct*, trabecular cornu; *f*, basicranial fontanelle; *fa*, foramen for carotid artery; *fm*, foramen magnum; *fo*, foramen for olfactory nerve; *ir*, infrarostral cartilage; *j*, jugular foramen for IX and X cranial nerves; *l*, perilymphatic foramina; *m*, muscular process; *M*, Meckel's cartilage; *o*, otic process of palato-quadrates; *pf*, palatine foramen; *pq*, palato-quadrates cartilage; *sr*, suprarostal cartilage; *t*, trabecular cartilage; *v*, secondary fenestra vestibuli. **B.** Anterior portion of chondrocranium of *R. fusca* during metamorphosis. Lateral view. **C.** Skull of 2 cm. *R. fusca*, after metamorphosis. Dorsal view. Membrane bones removed from left side. *a*, Auditory capsule; *am*, anterior maxillary process; *an*, annulus tympanicus; *art*, articular process of palato-quadrates cartilage; *eo*, exoccipital bone; *f*, fronto-parietal bone; *fpo*, prootic foramen; *mx*, maxillary bone; *n*, nasal bone; *o*, olfactory cartilages; *on*, orbito-nasal foramen; *pa*, anterior ascending process of palato-quadrates; *pg*, pterygoid bone; *pl*, pterygoid process; *pm*, posterior maxillary process; *pp*, posterior ascending process of palato-quadrates; *pq*, palato-quadrates cartilage; *pt*, pterygoid process of palato-quadrates; *px*, premaxillary bone; *qj*, quadrato-jugal bone; *II*, foramen for optic nerve; *III*, foramen for III cranial nerve; *IV*, foramen for IV cranial nerve. (From Ziegler.)

tion to the cranium proper. They connect with the trabeculae by **anterior ascending processes** back of the olfactory region, and by **posterior ascending processes** opposite the end of the notochord.

The remaining portion of the skull, which develops from the visceral arches, is connected with the jaw, and will be described shortly.

The **infundibulum** and **pituitary body** lies within the **basicranial fontanelle**, which is the open space just anterior to the tip of the notochord. From now on, development continues mostly in the posterior portion of the cranium.

Figures 310 and 353 show how the auditory organ is formed by a connective tissue capsule which soon becomes cartilage, while the **mesotic cartilage** grows out posteriorly and laterally from the para-

chordal plate to unite with the auditory capsule ventrally, both anteriorly and posteriorly.

The **occipital cartilage** is a continuation of the mesotic cartilage which fuses with the auditory capsule, and leaves a small opening through which the IX and X cranial nerve pass. This opening is called the **jugular foramen**.

The **basal plate** is the name given to the floor of the posterior portion of the cranium, which consists of occipital and mesotic cartilages together with the parachordal plate.

The occipital cartilage extends dorsally around the neural cord to form the **foramen magnum**.

The auditory capsule remains open into the cranial cavity internally by a large foramen, but closes externally.

The trabeculae now grow across the basicranial fontanelle so that it becomes entirely closed. This closed portion is the floor of the cranial cavity. The trabeculae then extend laterally and form the lateral walls of the cranial cavity, thus separating the cavity from the orbits.

Cartilages from the trabeculae also extend dorsally across the mid-line in the anterior region, to form a narrow dorsal bridge, leaving a large **supracranial fontanelle** between this bridge and the supraoccipital region.

The internasal septum extends dorsally and becomes the anterior wall of the cranial cavity, while the trabecular cornua remain separate from the olfactory capsules, but connect anteriorly with the supraorbital or labial cartilages. During metamorphosis, however, both labial cartilages and anterior ends of the cornua disappear in front of the olfactory capsules.

True bones form late in the frog. The following bones are the more important which have developed from cartilage:

**Exoccipitals, or Lateral Occipitals.** These form from the posterior portions of the occipital cartilage and auditory capsule. The occipital condyles themselves as well as the median dorsal and ventral portions of the occipital region remain as cartilage.

**Pro-otics.** These form from the more anterior portion of the auditory capsules as well as from the basal plate and orbital region.

**Ethmoids.** These form in the anterior portion of the wall of the orbit. They then unite both above and below so as to form a band around the cranium, often also called the **sphenethmoid** or **orbito-sphenoid**.

**Quadrato-jugal.** The palato-quadrato cartilage forms bone only in the region of the lower jaw. Then a connection is formed with a membrane bone and these two together form the **quadrato-jugal**. All these bones form before metamorphosis, the ethmoids alone developing some weeks after metamorphosis has taken place.

**The Visceral Skeleton.** In the mandibular and hyoid arches, as well

as the three branchial arches, the various skeletal elements **appear as condensations in the mesenchyme**, which soon become cartilaginous.

First, a **short rod** appears in the mandibular arch, transverse to the axis of the embryo.

This divides the dorsal portion into the beginnings of the upper jaw or **palato-quadrate**, and the ventral portion which is the beginning of the lower jaw. The lower jaw elements become subdivided into **Meckel's cartilage**, which comes to form the true jaw, and the **infra-rostral cartilage**.

The **palato-quadrate** has grown rapidly, as already described, and then fused with the trabeculae.

When the tadpole is about twenty-one millimeters long, the posterior or quadrate portion of this same cartilage connects with the auditory capsule.

With metamorphosis, the mouth enlarges, and this pushes back many of these structures, while the part of the palato-quadrate which lies in the orbital region, softens and disappears to a considerable extent. The anterior connection of palato-quadrate and trabeculae becomes the future **pterygoid** and **palatine** regions. All these changes draw the jaw to the posterior portion of the cranium from its original anterior position.

The infra-rostral cartilages, which have fused together across the midline, now fuse with the Meckelian cartilages to form the apex or **mental portion** of the chin. The fused cartilages are now known as **mento-Meckelian cartilages**. As these ossify, they fuse with the dentary, which is really the chief membrane bone of the lower jaw. There is a small median element between the infra-rostrals which also fuses with them.

The **annulus tympanicus** is the outgrowth from the quadrate cartilage which surrounds the tympanic membrane of the frog. It does not complete its growth until long after metamorphosis.

The **hyoid arch**, like the three branchial arches lying posterior to it, makes its appearance as a pair of rods of dense tissue in the corresponding visceral arches, though not at the same time as the others.

The hyoid cartilage, also called the **ceratohyal cartilage**, extends dorsad and connects with the palato-quadrate immediately behind where the jaw articulates. Ventrally, it unites with the hyoid cartilage of the opposite side. (Fig. 354.)

The first branchial cartilage also unites in the ventral midline, while the remaining branchial arches do not unite in the midline ventrally, but have their lower anterior ends unite with the one lying immediately anterior to it, and, finally, they connect dorsally in a similar manner.

The **copula**, which is a medial element, then appears in the ventral

region of the pharynx between the hyoid and the first branchial, and connects the ventral ends of both these arches.

The **hypo-branchial plate** consists of the lower ends of the first branchials which have become flattened and expanded. The ventral ends of the other three branchials fuse with the hypo-branchial plate.

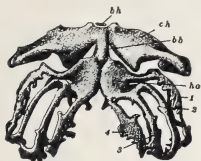


Fig. 354.

Hyoid and branchial arches of a 29 mm. larva of *R. fusca*. Ventral view. *bb*, Basibranchial (first), or copula; *bh*, basihyal; *ch*, ceratohyal; *ho*, hypo-branchial plate; 1-4, first to four cerato-branchials. (From Ziegler.)

The **cerato-branchials** are the lateral and middle sections of the branchial cartilages between the visceral pouches which remain separate from one another.

At metamorphosis, when the gill slits close, many changes naturally must take place in the structures just described. For example, the hyoid bar loses its connection with the palato-quadrates, and becomes smaller in diameter, while the copula likewise becomes smaller and a pair of new cartilages develop on each side of it, which then connect the hypo-branchial plate with the hyoid portions. These are the **manubrial cartilages**.

The **hyo-branchial apparatus** of an adult frog is made up of a broad median plate of cartilage which has been formed by the fusion of manubrium, copula, and hypo-branchial plate. The hyoid cartilages remain as slender processes called the **hyoid cornua**. The remaining portions practically disappear.

**The membrane bones.** In those portions of the cranium where considerable stretching has taken place, such as in the roof of the skull and the lining of the mouth, the substance is thinner than in the cartilaginous portions, and is then called **membrane**.

Membrane is nothing more than stretched-out-cartilage.

**The Parasphenoid.** This is a single median bone, and the first of all bones of the skull to appear, whether cartilaginous or membranous. It forms in the roof of the mouth when the tadpole is about twenty millimeters long. The parasphenoid becomes dagger-shaped and covers the entire basicranial fontanelle.

**The frontals and parietals**, which are paired, appear later and cover the supracranial fontanelle. They later fuse to form the fronto-parietals.

The **nasals** form the roof of the olfactory capsules and the **septonasals** or **intra-nasals** appear within the capsules.

The **premaxillae** and **maxillae** are the membranous parts which become the margins of the upper jaw.

The **dentary** and **angular** cartilages surround Meckel's cartilage; the dentary connects with the infra-rostrals of Meckel's cartilage.

The **vomers** are paired, and appear beneath the olfactory capsules.

The **palatines** form across the anterior margins of the orbits.

The **pterygoids** form along the inner faces of the palato-quadrates cartilages.

The **squamosals** form along the outer face of the palato-quadrate cartilages, and ultimately reach back to the auditory capsules. The **quadrato-jugal** is that portion which has developed at the posterior angle of the palato-quadrate cartilage and then fused with the quadrate bone. This is the only one of the membranous bones which cannot be distinguished from the cartilaginous bones of the skull.

## CHAPTER XVIII

### MAMMALIAN EMBRYOLOGY

**I**N both the chick and the frog—the two forms we have thus far discussed—the eggs have passed out of the body of the mother. In the frog, the entire embryo developed **after** the egg left the mother. In the chick where fertilization is internal, development began before the shell was formed, so that an embryo, approximately twenty-four hours old, was already present when the egg was laid.

Now we shall deal with **viviparous animals**, that is, with those which give birth to living young.

It will be understood quite readily that in those cases where living young are brought forth, the development must take place within the body of the mother, but, even in viviparous animals there are subdivisions. One subdivision is made up of such animals as the duckbill, the Australian ant-eater, the Australian kangaroo, and the American opossum. In these animals, known as **Marsupials**, the female bears a pouch in the abdominal region in which the young are placed at a very premature age. In fact, in the opossum, the embryo may be only about eight days of age when it is born for the first time, so to speak. The mother then places it within the pouch or **marsupium**, and here the young continue their development until able to lead an independent existence.

In all the higher forms of mammals with which the student is familiar, fertilization is internal, as in the chick, and the embryo passes through a process similar to that of the chick, except that this embryonic process takes place within the mother's body.

There is, however, in viviparous animals no real yolk-supply as in both the chick and the frog egg. Consequently, there must be some kind of an arrangement by which the young not only become attached to the uterus of the mother, but there must also be an arrangement by which a blood-supply can pass from mother to offspring, thus taking the place of the nourishment which the yolk furnishes in egg-laying animals.

The mammalian egg, not possessing a yolk, is very small.

The **original development** of egg and sperm, however, is not very dissimilar to that already described for the chick.

Before entering into the study of mammalian embryology proper, it is well, at this point, to understand the terminology usually applied to the life-history of a mammal.

First, the period of **gestation** or true embryonic period. It is during this time that the embryo depends upon its connection with the mother's

uterus for nourishment. Gestation extends from the time of the fertilization of the egg to the time of birth.

Second, **parturition**, or the actual time of birth. The condition of the offspring at the time of parturition varies to a considerable extent. Some animals are born with the ability to walk and take reasonable care of themselves within a very short time after birth, while some are quite dependent upon their mother for a long time.

Third, the period of **adolescence**, which is that period of life in the young devoted entirely to growth and development. It extends from birth to sexual maturity.

Fourth, **adult life**, or the period of **sexual maturity**. During this period many physiological changes often take place in the individual, entirely aside from those of the reproductive system.

### FERTILIZATION

As the egg is thrown out of the **Graafian follicle** (Fig. 355), it passes into the **oviduct (Fallopian tube)** and is carried by the cilia in the oviduct to the uterus. If fertilization takes place, the sperm, which finds its way

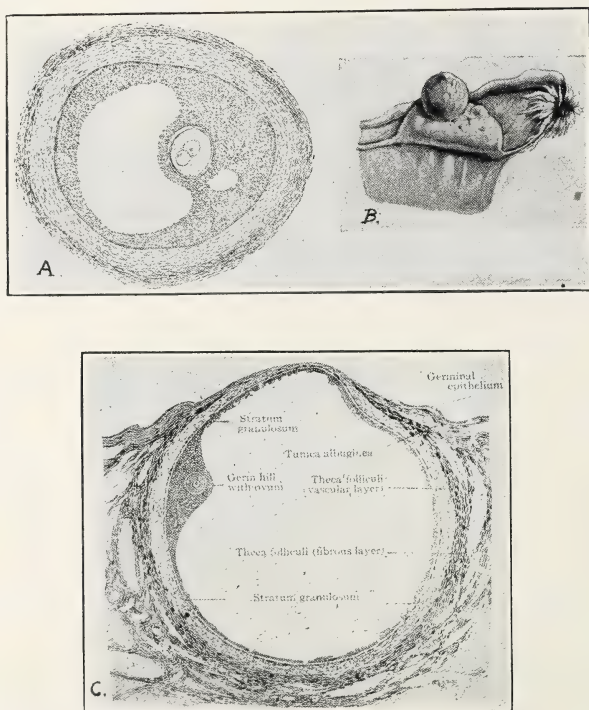


Fig. 355.

*A.* Section of well-developed Graafian follicle from human embryo (von Herff); the enclosed ovum contains two nuclei. *B.* Ovary with mature Graafian follicle about ready to burst (Ribemont-Dessaignes). *C.* Section of human ovary, showing mature Graafian follicle ready to rupture. *Kollmann's Atlas.*

into the uterus, passes into the oviduct in an opposite direction from that which the egg takes. This causes a meeting of egg and sperm. The length of time it takes the egg to reach the uterus, after ovulation, varies in different species of animals. It may vary from a few hours to several weeks. It is, therefore, practically impossible to state the exact time when fertilization actually takes place. This is especially true in the human being; but, as soon as the sperm does meet the egg, and fertilization does take place, the embryo begins developing. Consequently, by the time the fertilized egg reaches the uterus, it has already passed through, or is just passing through, a stage that is even a little advanced beyond the gastrula stage. There are, in fact, several germ-layers already present at this time.

### THE BLASTODERM

As soon as fertilization takes place, the egg divides equally into two cells, these two into four, and so on in the usual way. However, very early, some of the cells divide more rapidly than others, so that there is an overgrowth of those which grow most rapidly. This gives rise to several terms. The more rapidly growing, or **outer layer**, is called the **sub-zonal layer**, while the **central mass** is called the **inner cell mass**.

The sub-zonal layer is only one cell in thickness, so that it is easily distinguished from the inner cell mass. Then, too, a cavity forms between the two layers.

The entire structure is now called a **morula** (Fig. 356). As soon

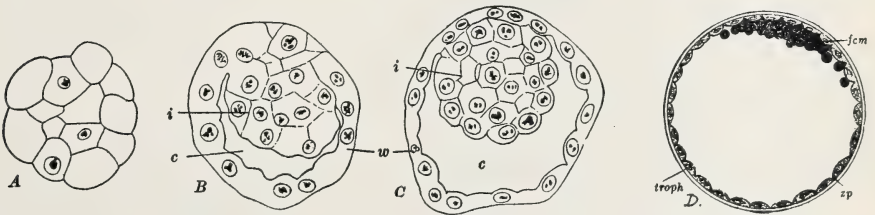


Fig. 356.

Morula and early blastodermic vesicles of the rabbit. The zona radiata and albuminous layer are not shown. *A*. Section through morula stage, forty-seven hours after coitus. *B*. Section through very young vesicle, eighty hours after coitus. Taken from uterus; ordinarily the ova have not reached the uterus at this age. *C*. Section through more advanced vesicle, eighty-three hours after coitus. Taken from uterus. *c*, Cavity of blastodermic vesicle; *i*, inner cell mass; *w*, wall of blastodermic vesicle (subzonal layer, trophoblast). (From Assheton.) *D*. Section through the fully formed blastodermic vesicle of the rabbit. *fcm*, Granular cells of the inner cell mass; *troph*, trophoblast cells; *zp*, zona pellucida. (From Quain's Anatomy, after Van Beneden.)

as the cavity has definitely formed between the inner cell mass and the sub-zonal layer, the morula is known as a **blastodermic vesicle**. This cavity contains a fluid which is supposed to represent the yolk-mass of the blastula and gastrula in the lower forms.

It will be noted from what has just been said that considerable development has already taken place by the time the fertilized egg reaches the uterus. Or, to repeat what was said above, it is as a **blastodermic vesicle** that the mammalian egg reaches the uterus after fertilization.

At this stage, two important points must be considered:

First, the method of the formation of germ-layers, and

Second, the method by which the blastodermic vesicle attaches itself to the uterus of the mother.

#### Formation of the Germ-layers.

The inner cell mass spreads out rapidly so as to form an inner lining to the sub-zonal layer. It is this inner lining which is the **entoderm**.

The sub-zonal layer becomes the **ectoderm**.

As there is a tremendous variation in the way germ-layers are formed in mammals, it may be well to think of the following example as a help in understanding some of these variations.

Suppose a group of football players who had already played together in previous years were to come together again. Each would immediately take his place without any preliminary instruction. So, we may think of the embryonic cells in the higher mammals taking a definite place and then developing from there on, rather than passing through all the stages of gastrula formation. This gastrula then actually indents to form two layers. That is, we may think of those embryonic cells which are to develop into ectoderm and mesoderm actually taking the proper position to develop into these structures without first becoming a single sheet and then indenting.

This would mean that the undifferentiated cells, which are to become ectoderm, would arrange themselves on the outer portion, those which are to become entoderm would arrange themselves more inwardly, and those which are to become mesoderm would take their place between these two layers, and then all three could begin developing at about the same time and grow simultaneously.

In the lower mammals, such as the cat, dog, rabbit, etc., this inner cell mass (entoderm) keeps pace with the sub-zonal layer, so that the original cavity, which has formed between the inner cell mass and the sub-zonal layer, is now surrounded by an inner layer of entoderm, while the outer layer still remains sub-zonal. In the higher forms, such as the primates, that is, in man and the higher apes, the inner cell mass does not grow as rapidly as the sub-zonal layer. There is, therefore, a second cavity formed within the inner cell mass of entodermal cells.

It is the remaining portion of the inner cell mass, after the entoderm has thus separated from it, which is the ectoderm. The sub-zonal layer is then called the **trophoblast** (Fig. 356, D). This trophoblast serves as the attachment of the blastodermic vesicle to the walls of the uterus.

We see from what has been said that a true mammalian gastrula

(although formed in a different manner from either that of the chick or the frog) has been established with two definite cell or germ-layers:

## ATTACHMENT OF THE BLASTODERMIC VESICLE TO THE UTERINE WALL

There are two general ways in which the blastoderm may become attached to the uterus.

The trophoblast or sub-zonal layer may remain as an outer layer around the entire blastoderm, or the developing embryo within the inner cell mass may push through this outer layer and come to lie in close relationship to the uterine wall.

At about the same time that attachment of blastoderm and uterine wall takes place, the **amniotic cavity** is formed (Fig. 357). The

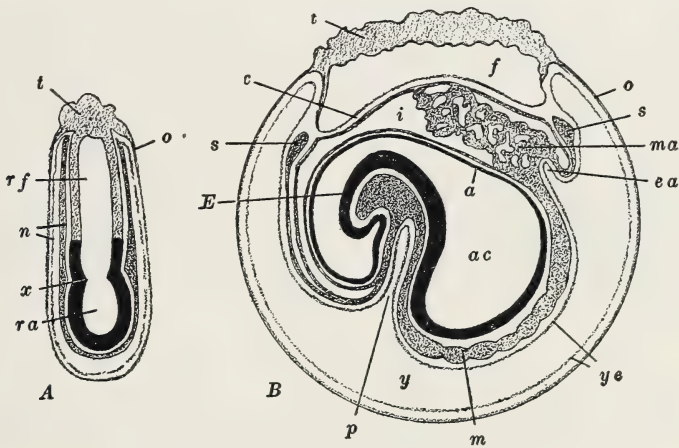


Fig. 357.

Diagrams of the relations of the cavities and layers in the rat, showing the "inversion" of the germ layers. Median sagittal sections. Embryo and amnion, black; ectodermal knob or "träger" in light tone; endoderm and mesoderm in darker tone. *A*. Early stage before the formation of the false amniotic cavity. *B*. Late stage showing false and true amniotic cavities and the interamniotic cavity. *a*, Amnion; *ac*, true amniotic cavity; *c*, chorion; *E*, embryo (anterior end; *ea*, endodermal rudiment of allantois); *f*, false amniotic cavity; *i*, interamniotic cavity; *m*, mesoderm; *ma*, mesoderm of allantois; *n*, endoderm; *o*, trophoblast (ectoderm); *p*, anterior intestinal portal; *ra*, rudiment of true amniotic cavity; *rf*, rudiment of false amniotic cavity; *s*, marginal folds. *t*, "träger" (ectoderm); *y*, yolk-sac; *ye*, yolk-sac endoderm; *x*, amniotic folds. (After Salenka.)

trophoblast remains as an outer covering in man, in many primates, and in such animals as the mouse, rat and guinea pig. When the trophoblast remains as the complete outer covering such a condition is known as **enttypy**, and it is in animals in which this condition occurs, that a definite space is formed between the germ layers and the trophoblast. This cavity is known as the **amniotic cavity**.

Sometimes the trophoblast thickens in this particular region and

a second or **false amniotic cavity** may develop. Figure 357 will make this clear.

In those cases, however, where the embryo pushes through the trophoblast and comes to lie as a disc upon its surface, the amnion is formed quite as it is in the chick.

The region in which the embryo develops is known as the **embryonic shield**. The **primitive head-node** lies practically in the middle of the embryonic shield. The **primitive streak** and the **primitive grooves** form quite as in the chick, and all structures lying anterior to the head-node lie in the head proper.

A definite **notochord** also forms, and the **neurenteric canal** can be seen quite plainly at the posterior limits of the embryonic rudiment.

Scarcely more than half a dozen human embryos have been seen prior to the time of the formation of the medullary plate. Then, too, none of these were of the same size, so we do not even have a basis for valid comparison, and consequently, we are unable to judge whether any of these were normal in size and form.

Mesoderm is formed in the mammal as it is in the chick, each mesodermal somite dividing into a somatic and a splanchnic layer. A layer of entoderm joins with the splanchnic mesoderm to form the yolk-sac, although no yolk is present. The trophoblast joins with the somatic mesoderm to form the **chorion**.

Here we may note that the term "ovum" is used in mammalian development to designate any early stage in the embryo, even to the inclusion of the entire blastodermic vesicle. The term "embryo" in man is given the embryo only **during the first two months of its existence**; thereafter (that is, when the face and body are quite well formed) it is known as a "foetus."

The smallest human embryo yet seen was 1.54 mm. in length, while the entire blastoderm was about 1 cm. in diameter.

## IMPLANTATION

There are three methods by which the blastoderm attaches itself to the walls of the uterus:

First, by what is called **central implantation**. This occurs in the ungulates and carnivores as well as in the lower primates and in some rodents, such as the rabbit. In these the blastoderm becomes superficially attached to the uterine wall, and, consequently, projects freely into the lumen of the uterus.

Second, **eccentric implantation**. This type is found in the mouse and in some insectivora. In these forms the blastodermic vesicle lies in a furrow or groove in the uterine wall. This groove is then closed up so that the vesicle comes to lie in the walls of the uterus.

Third, **interstitial implantation**. In this type the blastodermic vesicle actually burrows its way into the mucous membrane lining of the uterus.

It is this third type which occurs in man and in some of the rodents, such as the guinea pig and the gopher.

The trophoblast, in the region where it is to meet with the uterine wall, has become highly specialized physiologically in the eccentric and interstitial types of implantation. Its cells form a layer of considerable thickness, and it is then called a **trophoderm** (Fig. 358). These cells are supposed to dissolve, or digest, the uterine mucosa so as to permit a definite implantation and also, probably, to digest some of the mucosa as food for the growing embryo.

The blastoderm attaches itself to the uterine wall between the two oviducts, and it is in the region of implantation that the maternal tissues come into contact with the embryo. We must, therefore, look for the beginnings of the **placenta** in this region.

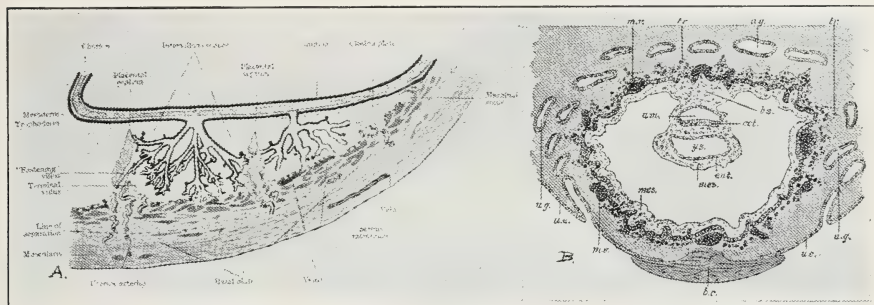


Fig. 358.

- A. Diagrammatic section of placenta. (After Strahl, Bonnet.)  
 B. Section through an embryo of 1 mm. embedded in the uterine mucosa (semidiagrammatic after Peters). *Am.*, amniotic cavity; *b.c.*, blood-clot; *b.s.*, body-stalk; *ect.*, embryonic ectoderm; *ent.*, entoderm; *mes.*, mesoderm; *m.v.*, maternal vessels; *tr.*, trophoderm; *u.e.*, uterine epithelium; *u.g.*, uterine glands; *y.s.*, yolk-sac.

In fact, it is the trophoderm which later becomes vascularized from the mesoderm of the chorion or allantois, to act as the chief absorptive surface through which, and by which, material from the maternal tissues and blood is taken to the embryo.

## THE EMBRYONIC MEMBRANES

It will be remembered that in the chick embryo, the amnion has as one of its functions the protection of the embryo from drying and from becoming deformed by the outer shell pressing against it. The chick's yolk-sac contains a large quantity of food-substance which the developing embryo uses, and the allantois serves as a respiratory and (partially) as an excretory organ. In the chick the serosa or chorion was of little importance.

In the mammal it is the amnion which is of secondary importance.



But as the student must know the placental animals in order to make the most of his study in Comparative Anatomy, it is essential that he at least obtain a clear and accurate understanding of the two principal types of placental formation.

In the first place, the placenta may be defined as consisting of all **structures affecting nutritive, respiratory, and excretory interchanges between the embryo and its mother** in viviparous animals. It is evident, then, that the placenta must form in the region where the trophoblast comes in contact with the uterine mucosa, and that the trophoderm itself, plus the vascularization in the yolk-sac, allantois, or chorion, will be the elements from which the placenta is developed. (Figs. 358, 359.)

At this stage the student must review the chapter on the development of the extra-embryonic membranes in the chick.

The rabbit is often used as an example of a form of mammalian embryology which can be contrasted with the embryological development of the chick. In the rabbit the extra-embryonic membranes develop quite like those in the chick, except that the point of fusion of these membranes consists of only a small knot, whereas in the chick this fusion takes the form of an elongated seam. In both rabbit and chick the tail-fold grows more rapidly than the head-fold.

In man, where entopy takes place (that is, where the trophoblast remains continuous about the entire blastoderm), the extra-embryonic membranes do not grow as in the rabbit and chick, but by a **splitting of the ectoderm to form the beginning of the amniotic cavity**.

The forming of the extra-embryonic membranes in man quite naturally causes the embryo to remain connected with the blastodermic wall by a **body-stalk** (Fig. 358, B). The separating of the ectoderm immediately above the embryo to form the amniotic cavity causes the embryo to form the **floor** of this cavity, while the trophoblast forms the **roof**. The sides, or **walls**, of the cavity meet the embryo at the edges of the embryonic shield.

But, whether the amniotic cavity is formed as in the rabbit or as in man, the walls of the cavity extend ventrally until they surround the umbilicus.

The yolk-sac and the yolk-stalk, as well as the allantois, although quite small in man, are pushed into this **body-stalk** or **umbilical-stalk**. The amniotic cavity grows large in man and contains from one-half to one liter of **liquor amnii**.

## THE YOLK-SAC

The open space on the interior of the mammalian blastodermic vesicle is supposed to represent the yolk-sac (Fig. 359, G) of such animals as the chick and the frog; and, as this open space is relatively very large, the yolk-sac occupies the main portion of the early mammalian blastodermic vesicle. The cavity of the vesicle opens into the mid-gut region

by the broad yolk-stalk just as with the chick. Its wall is separated from the chorion by the extra-embryonic **coelom**—also called the **exocoelom**. (Fig. 359, E.)

The amnion and chorion are formed from somatopleure, while the yolk-sac is formed from splanchnopleure.

The blood vessels and the sinus terminalis arise in the yolk-sac of the rabbit just as they did in the chick.

In the higher primates, including man, the yolk-sac never fills the entire blastodermic vesicle and is very slow to grow. In fact, during the first month it has a diameter about the length of the embryo, and after increasing this diameter to a little over a centimeter, it decreases in size. The yolk-stalk is formed, however, and elongates considerably to enter the proximal end of the umbilical cord.

The amniotic membrane now expands and pushes against the exocoelom until that is eliminated and the yolk-sac disappears in the placental region. The yolk-stalk itself becomes a solid cord during the second month. However, the proximal end sometimes remains open. In such a case it appears as a diverticulum from the intestine and is called **Meckel's diverticulum**.

### THE ALLANTOIS

This structure also varies in size to a considerable extent, from filling the entire exocoelom as in the lower primates such as the Lemurs, to occupying but a small portion of the umbilical cord as in man and the higher primates (Fig. 359, G).

The early development of the allantois in the mammals is quite similar to that in the chick, but its later development is varied, the variation being ascribed to the changed conditions brought about by the formation of placental structures.

The later history of the allantois is limited to the placental structures **only**. In the rabbit the allantois extends into the exocoelom and comes in direct contact with the chorion in the region where chorion and uterus unite. It thus lies in the direct pathway of connection between mother and offspring. Blood vessels now develop in the allantoic mesoderm to form the umbilical arteries and the umbilical veins, and it is through these allantoic blood vessels that the **embryonic circulation** is related to the **placental circulation**.

In man the development is quite different; for, here there is nothing which interrupts the connection of chorion with the maternal tissues. The way in which the body-stalk develops in man has been described already. This is often said to be equivalent to a modified allantoic stalk. There is, therefore, in man, **no true allantois as a free vesicle**. Only a small tubular outgrowth from the entodermal lining of the yolk-sac can be seen, and this outgrowth, in turn, is not distinguishable from the hind-gut. It extends into the body-stalk. As the embryo grows, and the

body-stalk extends, the allantoic stalk extends further along in the body-stalk as well, and so remains during foetal life (Fig. 360).

As the ventral body-walls of the embryo are formed and approach each other, the proximal end of the allantoic stalk becomes the **urinary bladder** and the beginning of the **urogenital sinus**. From the bladder region to the body-wall it is reduced as a mere solid strand of connective tissue known as the **urachus**.

Vascularization is quite alike in the various mammalian forms.

The development of the placenta depends upon the manner and type of implantation, which in turn causes different relationships between the growing embryo and the maternal tissues.

### THE DECIDUAL MEMBRANES

We have been describing the **embryonic placenta**. Now we shall describe the **maternal placenta**. There is a change which takes place in the lining of the uterine walls when the trophoderm unites with the uterus. The uterine lining which bulges out into the uterine cavity to cover the blastoderm, is called the **decidua capsularis** (formerly **decidua reflexa**), while the uterine lining at the point where blastoderm and uterus unite is called the **decidua basalis** or **decidua serotina**, the remaining portion of the lining being known as the **decidua vera** (Fig. 361).

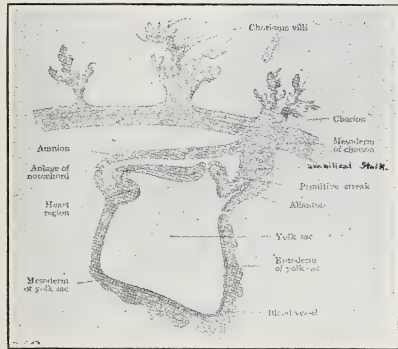


Fig. 360.  
Medial section of early human embryo.  
(After von Spee, Kollmann.)

the maternal tissues. Large **lacunae of blood** are formed in the maternal tissues by the syncytial tissue directly, or by the rupture of the blood vessels which are under great pressure in this region.

The trophoderm then thickens at intervals and forms little villi or finger-like projections, and the chorionic mesoderm grows out into these villi so that there is a branching of the **primary villi** into **secondary villi** or **true villi** (Fig. 358).

In the meantime the blood lacunae run together and surround and bathe the villi, while the trophoderm, which began as a spongy network, is now a continuous layer covering the entire outer surfaces of the villi and chorion.

Branches of the umbilical vessels develop in the mesoderm of the

chorion and villi. This means that there are now two layers of epithelium covering the mesodermal core of all the villi, and that it is in these villi that the chorionic circulation of the embryo is established.

The blood vessels of the uterus open into the little blood-lacunae, which is another way of saying that the syncytial trophoderm, which covers the villi, is bathed in maternal blood. This is where the nourishment of the embryo takes place. The maternal blood itself does not pass into the developing embryo.

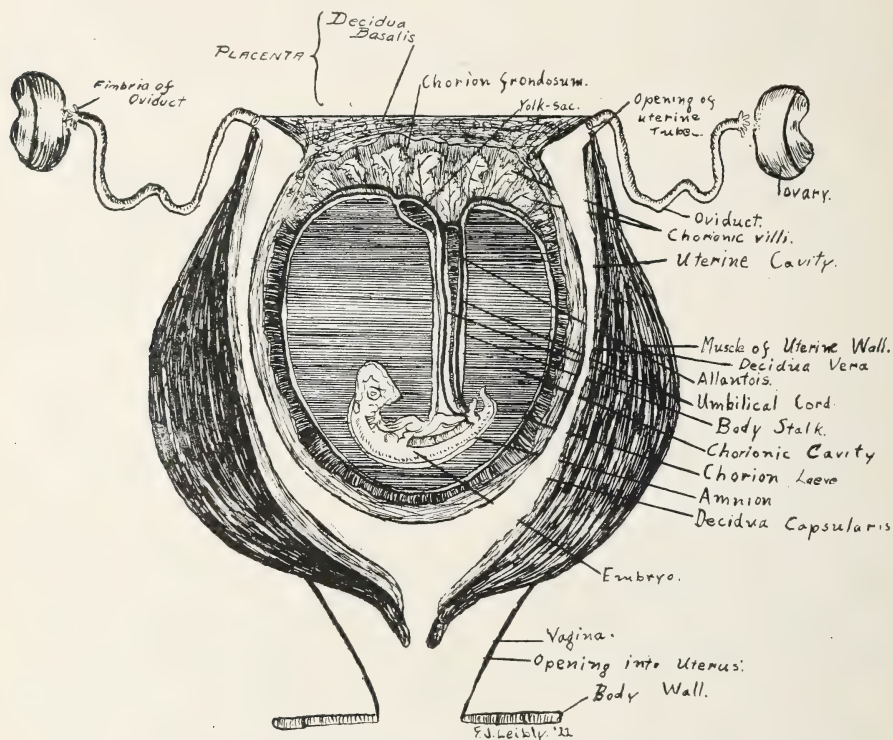


Fig. 361.

Diagram to show relationship of mammalian embryo and maternal membranes.

At first the villi cover the entire surface of the chorion, but in man, after a few weeks, the villi located away from the point of attachment begin to degenerate and finally leave that portion smooth. This smooth region is called the **chorion laeve**, while the attached portion, which retains the villi, is known as the **chorion frondosum** (Fig. 362). It is the chorion frondosum, together with the decidua basalis, which constitutes the **placenta**. And it is the chorion frondosum to which the embryo is attached by the body-stalk which later comes to be called the **umbilical-stalk** or **umbilical cord**.

The decidua basalis forms what is called the **maternal placenta**, and the chorion frondosum the **foetal placenta**.

The decidual membranes and their attachments form the **after-birth**. This afterbirth consists of amnion, chorion, decidua vera, placenta, and a part of the decidua basalis.

## THE UMBILICAL CORD

As the body-stalk becomes longer and longer, finally reaching a length of some fifty centimeters, there must be some circulatory connection between the embryo and the chorion frondosum. This connection is brought about by the development of four blood vessels, two veins and two arteries, known as the **umbilical vessels** or **allantoic vessels** (Fig. 363). The two veins push their way into the embryo to open into the heart. The arteries likewise grow in the same direction as do the veins, but connect with the dorsal aorta. Their distal ends extend

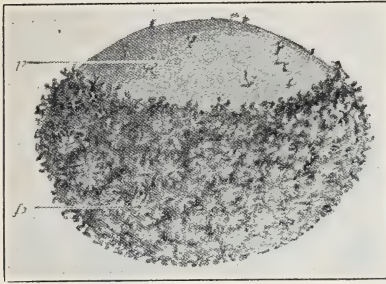


Fig. 362.

Human Embryo. Age seven weeks. (From Kollmann.) *cf*, chorion frondosum. *cl*, chorion laeve.

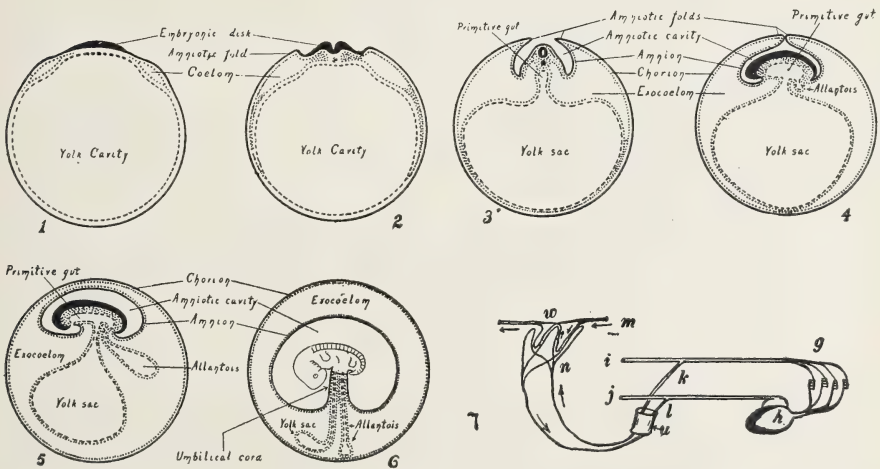


Fig. 363.

1 to 6, Diagrams representing six stages in the development of the foetal membranes in a mammal.

The ectoderm is indicated by solid black lines; the endoderm by broken lines; the mesoderm by dotted lines and areas. (After Kölliker.)

7, Diagram of nurture of young through embryonic membranes. *g*, gill circulation of embryo; *h*, heart; *i*, dorsal aorta; *j*, postcava; *k*, allantoic artery; *l*, allantoic vein; *m*, indicating the course of the blood of the mother, parallel to *n*; *n*, that of the embryo; *u*, umbilical cords; *w*, wall of uterus. (After Needham.)

through the body-stalk into the villi to connect with the vascularization there established.

The two veins later fuse, so that a cross section of a mature umbilical cord (Fig. 364), shows two arteries and a single large vein.

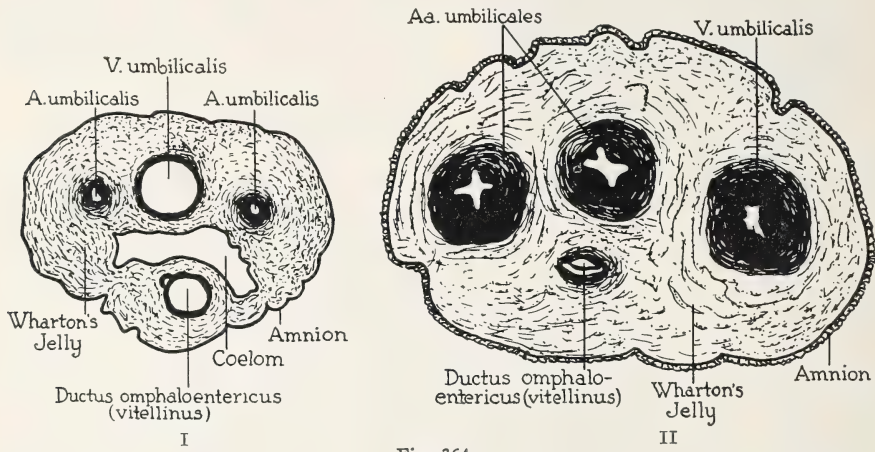


Fig. 364.

I, Umbilical cord of human embryo at three months.  
II, Same at birth. (After Corning.)

In addition to the umbilical vessels just mentioned, the yolk-stalk (in the early stages only), and the allantoic stalk can be seen in cross sections of the cord, while the cord itself is filled with a mesenchymal, mucous-like substance, called **Wharton's jelly**.

The cord is twisted and is attached to the **umbilicus** or **navel** of the foetus and to the placenta. The outer covering of the umbilical cord is a layer of ectoderm which is continuous with that of the amnion of the embryo.

The following table shows the relative increase in size and weight of the human embryo and foetus throughout the period of gestation:

	Weight	C. H.	Length*	C. R.
Ovum (estimated) .....	0.000004 grm.	.....	.....	.....
23 days .....	0.04	2.5 mm.	.....	2.5 mm.
56 days .....	3.0	30.0	.....	25.0
84 days .....	36.0	98.0	.....	68.0
112 days .....	120.0	180.0	.....	121.0
140 days .....	330.0	250.0	.....	167.0
168 days .....	600.0	315.0	.....	210.0
196 days .....	1000.0	371.0	.....	245.0
224 days .....	1500.0	425.0	.....	284.0
252 days .....	2200.0	470.0	.....	316.0
270 days .....	.....	500.0	.....	336.0
280 days .....	3200.0	.....	.....	.....

\*C. H.=Length as measured in a straight line from the crown of the head to the heel.  
C. R.=Length from crown to rump or sacral flexure.

If the student has thoroughly mastered the subject-matter of this semester's work in embryology he will not only be able to understand how a normal embryo develops, but he will also know how and why many and varying types of abnormal development occur by either mechanical or chemical injury of some kind, which injury may cause any portion of the embryo to stop growing, while other parts continue in the usual manner. Monstrosities of many kinds may thus be formed, and even in apparently normal individuals it is by no means rare for the surgeon to find individual internal organs underdeveloped or overdeveloped. All such deviations from the normal are of the utmost importance to the medical man, and it is only through a study of embryology that they are made understandable.

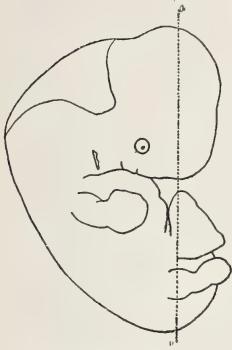


Fig. 365.  
Figure to illustrate the  
"vertex-breech" method of  
measuring human embryos.  
a-b, vertex-breech length of  
the embryo.



**PART II**  
**Comparative Anatomy**



## CHAPTER XIX

### INTRODUCTION TO COMPARATIVE ANATOMY

**I**N the study of Comparative Anatomy a method somewhat different from our study up to this moment must be brought into play.

In the forepart of this book, the frog was studied as a **type-form of vertebrates**, and the earth-worm as a **type-form of annelids** as well as of **coelomates**, and then, **after** each such type-form had been studied, it was compared with other forms likewise studied in the laboratory.

Now we are to take an **entire system in each of the leading groups of vertebrates and compare system by system**, always **reviewing the development** of the particular system studied, and comparing such development with the development of the respective systems in both frog and chick, as shown in **Part One** (embryology) of this book.

Three distinct points of view must be kept in mind in Comparative Anatomy, namely, those of:

**Structure (both gross and microscopic).**

**Development (embryology).**

**Comparison of organ systems.**

Just as in any account of man's history we attempt to study those races which we now consider as living under primitive conditions, believing that they will throw some light upon the problems that our ancestors had to overcome in order to bring about our present state of civilization, so, in Comparative Anatomy we attempt to study the so-called lower-animal life in order that this may throw light upon the development of our own bodies. This may be brought home the better by remembering that all higher forms of life practically possess all organs and system of organs which the lower forms possess **plus an additional something**. This does not prove by any means that any of the higher systems must have necessarily come from the lower. All it does mean is that all forms of animals, which walk on the earth, must have much that is similar. For instance, legs used for the same purpose in all animals must have muscles that will function alike; because, regardless of what position we systematically assign these animals, they, by virtue of the fact that they walk, must necessarily have leg muscles, and having these, there must be a supporting structure for such muscles, so that the skeletal systems of walking animals will be closely akin.

Comparative Anatomy proper, then, will consist of a comparison of the organ systems of four great groups of vertebrates. The classic examples used for such comparison are:

The **dogfish**, as an example of a group of living organisms whose skeletal tissues are largely cartilaginous.

The **turtle**, as an example of the **reptilia**.

The **cat**, as an example of the **mammalia**.

The **frog**, as the classic example of the **amphibian**. This animal has already been studied in the early part of the course, but must be kept in mind so as to be compared with the above three types.

It is usual to exclude the **aves**, because **reptile** and **bird** have so many structural similarities that the study of one suffices for that of the other. In fact the single word **Sauropsida** has come into common biological usage as meaning both **reptiles** and **birds**.

It is necessary, first, for us to have some conception of what is meant by the phylum **Chordata** and to appreciate that there are intermediate types between **invertebrates** and **vertebrates**. Such intermediate types are known as **pro-chordata**. The **pro-chordata** and the **vertebrata** together form what zoölogists call the phylum **Chordata**.

The **vertebrates** possess a **spinal**, or **vertebral**, column which consists of a great number of similar portions, called **vertebrae**, arranged in a longitudinal series. In the early embryo of all **vertebrata** there appears a rod-like **notochord**. This probably serves as a sort of stiffening to the animal, and in this respect only is it similar to the **spinal column** proper. It is neither **cartilage** nor **bone**, and probably develops from the **entoderm** or **mesoderm**. As the **spinal cord** develops from the **ectoderm**, and the **bones** of the **spinal column** from the **mesoderm**, it will be seen that neither of these three just-mentioned portions are alike in either origin, function, or position.

In all **vertebrates** the main nerve cord lies on the **dorsal side**, while in **invertebrates** it lies on the **ventral side**.

There are certain groups of animals which possess no **spinal column**, yet, during the **embryonic period** have a **notochord**, a **dorsal nerve cord**, and a **gill-slit apparatus** (Figs. 313, 314, 315, 316). The classic examples of these forms are **Amphioxus**, **Balanoglossus**, and the **tunicate** or **sea squirt**, all of which are comparatively small in size and live in the sea. These forms are grouped together under the name of **pro-chordata**. Professor Patton of Dartmouth College has described a scorpion in which he is sure he has found a **notochord**. If he is correct, it will be seen that no classification of this kind is absolute, in that **invertebrates** of very early geologic times may have possessed such an **embryological structure**.

## CHAPTER XX

### CLASSIFICATION OF FISHES, AMPHIBIANS, REPTILES, AND MAMMALS

**U**NLESS this chapter is mastered, there can be no understanding of the textual matter which follows, as the scientific terms there used are all based on what this chapter contains.

#### CHORDATA

The **Chordata** possess a notochord at some time during their life's history (the notochord lying between the nervous system and the alimentary tract), a hollow central nervous system lying entirely on one side of the digestive canal, and pharyngeal slits extending from the pharynx to the exterior.

The Chordata are divided into four sub-phyla, all of which develop a notochord during their embryonic period, though all do not later develop a bony vertebral column.

The subdivisions of the Chordata (Figs. 313, 314, 315, 316) are as follows:

##### **Sub-Phylum I. Cephalochordata (Adelochorda, Fig. 312).**

The notochord runs only up to the head proper in most chordates, but in the **Cephalochordata**, of which **Amphioxus** is the classic example, the notochord extends to the very anterior end of the body. **Amphioxus** is fish-like in form and is used as an example of the most primitive form of the chordates. It will be remembered that there was reference made to the simplicity of the embryology of **Amphioxus** in the early part of this book.

**Amphioxus** has no skull or vertebral column. The pharyngeal slits are quite numerous. The true scientific name of **Amphioxus** is **Branchiostoma**. In popular language it is often called **lancelet**, on account of its sharp, lance-like appearance.

##### **Sub-Phylum II. Urochordata (Tunicates, Figs. 312, 313).**

This group possesses a notochord only in the caudal region. The young are tadpole-like, and there is a metamorphosis converting the tadpole into a sac-like structure.

**Order 1. Larvacea (Appendicularia)**, free-swimming forms with permanent tail.

**Order II. Ascidiacea (Tunicates or Sea-Squirts)**, fixed forms without tail in the adult.

**Order III. Thaliacea (Salpians)**, free-swimming forms without tail in the adult.

The neurenteric canal is permanent.

### Sub-Phylum III. Hemichordata (Fig. 314).

A rather doubtful form. There is a projection from the mid-dorsal region of the digestive canal which looks somewhat similar to a notochord. These animals have a collar and a proboscis.

**Order I. Enteropneusta**, which include worm-like forms such as *Balanoglossus*.

**Order II. Pterobranchiata**, sessile, tube-dwelling forms such as *Cephalodiscus*, and *Rhabdopleura*.

**Order III. Phoronida**, tubed forms such as *Phoronis* (Fig. 199).

### Sub-Phylum IV. Vertebrata (Craniata).

1. The vertebrates show their segmentation in the adult form only on the interior of the body, as for example, the metameric arrangement of myotomes, sclerotomes, etc.

2. A cuticular skeleton is absent, but there may be cornifications of the epithelium, or ossifications in the dermal regions, such as the scales of fishes, etc.

3. An axial skeleton is present, consisting of skull and vertebral column.

4. There are two kinds of appendages supported by the axial skeleton, namely, the unpaired fins (which occur only in fishes and Amphibia), and the paired appendages (anterior and posterior), which are usually present.

5. The central nervous system is dorsal in position. The brain itself consists of five parts: the cerebrum, "twixt-brain," mid-brain, cerebellum, and medulla oblongata.

6. Of the sensory organs, the eyes and ears are the most highly developed.

7. The respiratory organs arise from the entoderm of the pharynx. Pharyngeal slits are present in the embryo. In terrestrial animals these pharyngeal slits are later functionally replaced by lungs which develop from the hinder portion of the pharynx.

8. The heart lies ventrally in the pericardium. In gill-breathing species it contains only venous blood, but in lung-breathing animals it is divided into venous and arterial halves. The circulation is closed.

9. The sexes are usually separate, while in most species the excretory (nephridial) system forms the ducts for the reproductive (genital) system.

10. Reproduction is strictly sexual.

The classes of Vertebrata are as follows:

#### Class I. Cyclostomata (Fig. 366).

These are the round-mouthed eels without a lower jaw. Examples are the lampreys and hagfishes. It is in this group that we find the only vertebrate parasites.

There is a primitive skull, but no true vertebrae (only bony arches). Paired fins, true scales, and teeth are lacking. The gill-pouches are saccular and the nose is unpaired.

**Sub-Class I. Myxinoidea** (Fig. 366).

These are the "hag-fishes" or "borers" which give off a slimy,

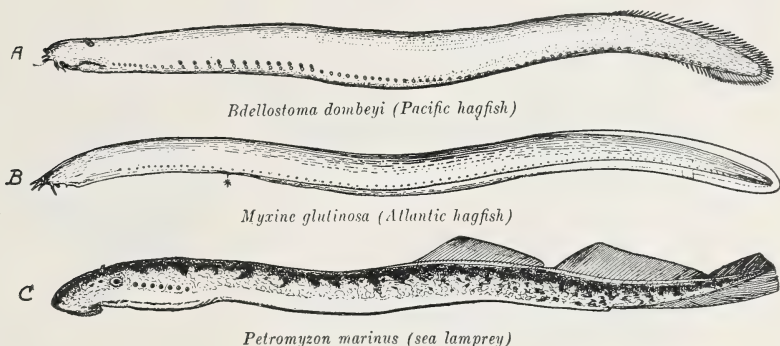


Fig. 366.

Cyclostomes. The light openings along the sides are mucous canals, the dark ones are branchial openings.

mucous jelly when captured. It is from this fact that they receive their name of **Myxinoidea**.

**Sub-Class II. Petromyzontia** (Fig. 366).

These are the lampreys. They live in both salt and fresh water. The **myxinoids** attack principally dead and disabled fishes, but the **petromyzons** attack decidedly active fish much larger than themselves, attaching themselves to their host and making great inroads with their rasping tongues.

**Class 2. Pisces (Gnathostomata).** All fish having true lower jaws.

Fishes are distinguished from the **Cyclostomes** not only by having true lower jaws but also by having a vertebral column (**amphicoele vertebrae**, Fig. 404); by having scales, paired pectoral and pelvic fins, and paired nostrils. They breathe by gills and have a heart with venous blood therein only, although the heart has auricle, ventricle, sinus venosus, and some have a conus arteriosus.

**Sub-Class I. Elasmobranchii.**

These are the sharks and their near relatives. They have a cartilaginous skeleton, usually a heterocercal tail, placoid scales (thornlike), but in **Mustelus** (the dog-shark, which is used in the laboratory), pointed, overlapping scales. There are five to seven slit-like gill-openings on each side. The eggs are few and hatched within a sac inside the body. The **skates** belong to this group as they are merely flattened out sharks.

There are various extinct orders and sub-orders of elasmobranchs, but we shall deal only with two orders and two sub-orders.

### Order Plagiostomi.

**Sub-Order I. Selachii** (twelve living and three extinct families of sharks and dog-fishes, Fig. 367).

**Sub-Order II. Batoidei** (Saw-fishes, skates, rays and torpedoes, seven families, Fig. 367).

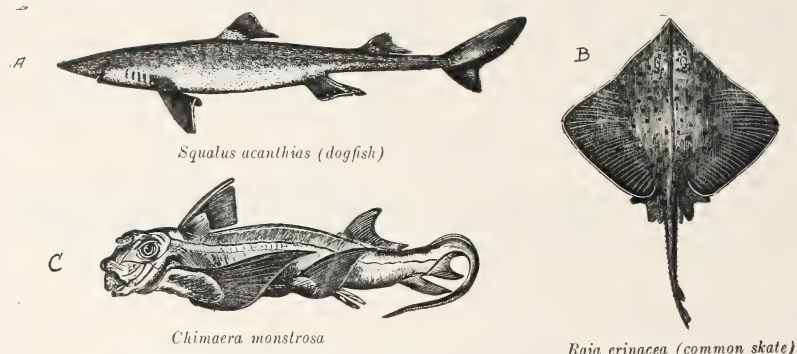


Fig. 367. Elasmobranchii. (A, after Goode; C, after Claus.)

**Order Holocephali** (Chimaera, Fig. 367, one living and three extinct families).

The Holocephali are very grotesque looking animals and are of great antiquity. There are peculiar grinding plates in the mouth instead of teeth.

### Sub-Class II. Teleostomi. (The true bony fishes.)

Skeleton partly or entirely bony, a single gill-opening on each side leading to gill-arches on which there are gill filaments. There is also a swim-bladder which may disappear with age.

In the higher forms where the skeleton is entirely ossified, the pelvic girdle approaches the pectoral one, so that the pelvic fins may be directly beneath the pectoral fins. It is the approach of the girdles and fins which is used in classifying fish, because this is supposed to show different degrees of specialization.

The position of the fins in the higher fishes is supposed to furnish evidence to show that amphibians and higher fishes are not closely related.

### Order I. Crossopterygii.

**Sub-Order I. Osteolepida.** (Four extinct families.)

**Sub-Order II. Cladista.** *Polypterus* and *Calamichthys* are the usual examples. (Fig. 368.)

### Order II. Chondrostei. (Five extinct and two living families.)

These include the paddle-fishes and sturgeons (Fig. 368).

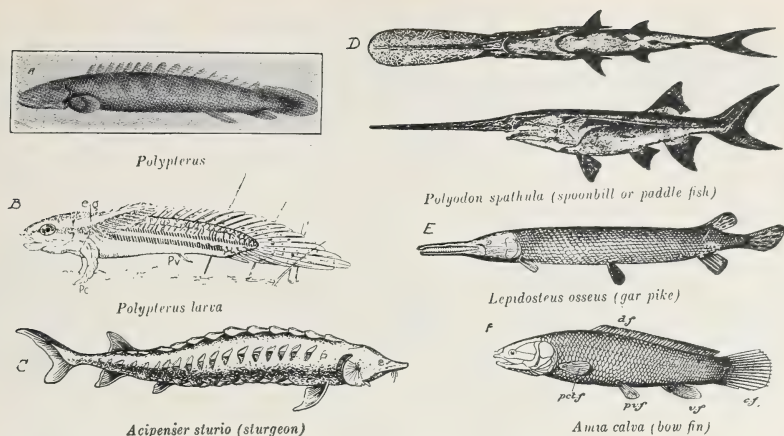


Fig. 368. Ganoids.

In *B*, e.g., Large external gill of the hyoid arch; *Pc.*, pectoral fins; *Pv.*, pelvic fins. The larva is drawn in a very characteristic attitude.

In *C* note the elongated snout, the barbules bounding the ventral mouth, the operculum covering the gills, the rows of bony scutes, the markedly heterocercal tail.

*D*, Ventral and side view.

*F*, *Amia calva* (Bow fin). *c.f.*, caudal fin; *d.f.*, dorsal fin; *pct.f.*, pectoral fin; *pv.f.*, pelvic fin; *v.f.*, ventral fin. (*B*, after Budgett; *D*, after Goode; *E*, after Tenney; *F*, after Günther.)

### Order III.<sup>1</sup> Holostei. (Six extinct and two living families.)

These include the bow-fins and gar-pikes. (Fig. 368.)

### Order IV. Teleostei.

#### Sub-Order I. Malacopterygii (21 families).

These include tarpons, herring, salmon, etc. (Fig. 369.)

#### Sub-Order II. Ostariophysii (six families).

These include carp, tench, cat-fishes, etc. (Fig. 369.)

#### Sub-Order III. Symbranchii (two families).

A small group of eel-like fishes having characteristics of both

#### Ostariophysii and Apodes.

#### Sub-Order IV. Apodes (five families).

These are the eels. (Fig. 369.)

#### Sub-Order V. Haplomi (fourteen families).

These are the pickerel, killifishes (mud-minnows, etc.).

#### Sub-Order VI. Heteromi (five families).

These are the Fierasfer, etc. (Fig. 370.)

#### Sub-Order VII. Catosteomi (eleven families).

These are the stickle-backs, pipe-fishes, sea-horses, etc. (Fig. 370.)

#### Sub-Order VIII. Percosoces (flying fishes), (twelve families).

These include the Belone, sand-eels, rag-fishes, etc. (Fig. 370.)

<sup>1</sup>The student will meet with the term "Ganoid" in his reading. This merely refers to a shiny scale. In the United States the gar-pike (*Lepidosteus*) found in the Mississippi Valley, is commonly mentioned, although older writers made a distinct grouping of Ganoids, consisting of Orders I, II and III, using the African *Polypterus* as the classic example. In *Lepidosteus*, Ganoid scales have a sort of peg and socket arrangement.

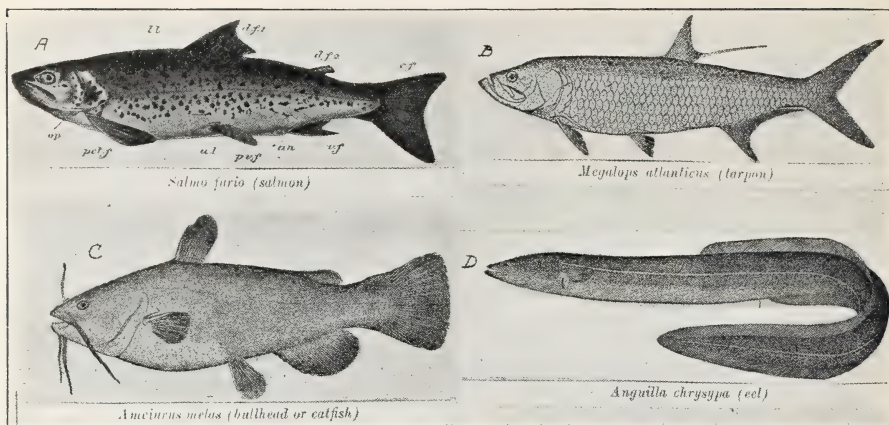


Fig. 369. Teleostei.

A, Brook Trout, a sub-genus of the Salmon family, *a.l.*, adipose lobe of pelvic fin; *an.*, anus *c.f.*, caudal fin; *d. f. 1*, first dorsal fin; *d. f. 2*, second dorsal or adipose fin; *ll.*, lateral line; *op.*, operculum; *pct.f.*, pectoral fin; *pv.f.*, pelvic fin; *v.f.*, ventral fin. (A, after Vardine; B and C, after Goode; D, from Bull. U. S. F. C. 1895.)

### Sub-Order IX. Anacanthini (three families).

These are the cod, etc. (Fig. 370.)

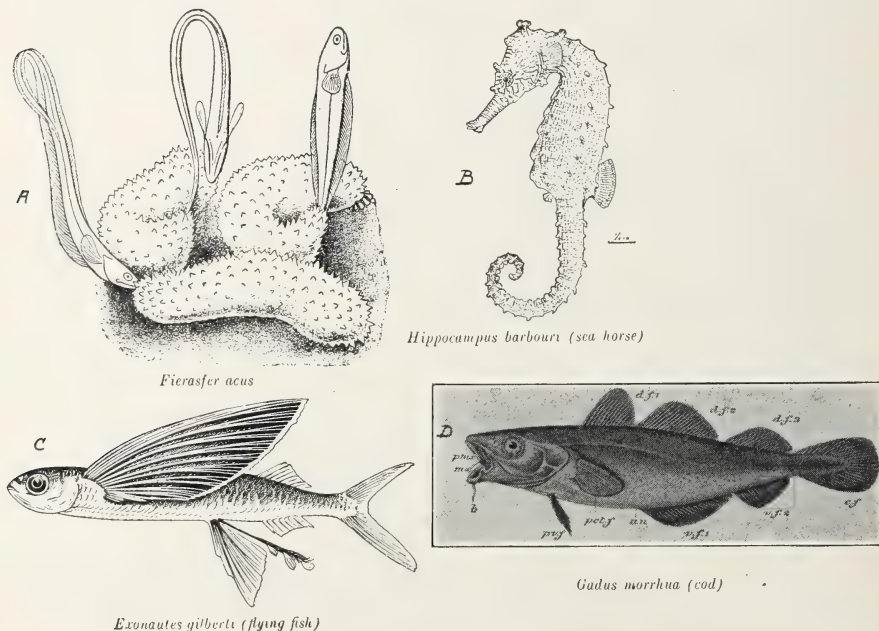


Fig. 370. Teleostei.

A, *Fierasfer acus* penetrating anal openings of holothurians. D, an, anus; *c.f.*, caudal fin; *d.f. 1-3*, dorsal fins; *m.x.*, maxilla; *pct.f.*, pectoral fin; *pmx.*, premaxilla; *pv.f.*, pelvic fin; *v.f. 1* and *2*, ventral fins. (A, after Emery; B, after Bull. U. S. F. C. 1907; C, after Jordan and Evermann; D, after Cuvier.)

**Sub-Order X. Acanthopterygii** (78 families).

These include a great majority of our more common fishes, such as perch, bass, mackerel, flounders, gobies, shark-suckers, climbing perch, etc. (Fig. 371.)

**Sub-Order XI. Opisthomi** (one family).

These are the eel-like fishes.

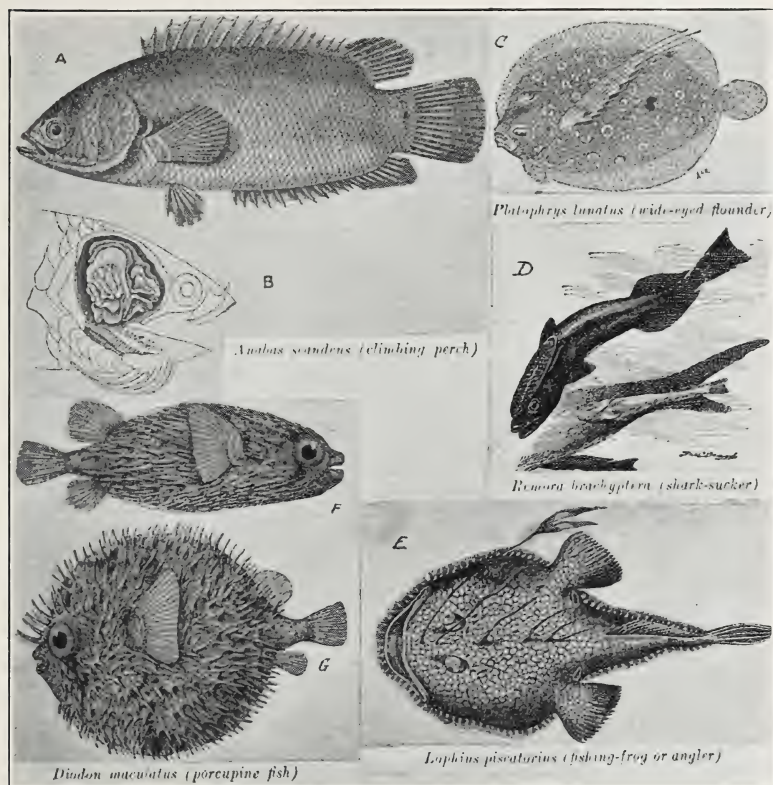


Fig. 371. Teleostei.

B, Dissection of head of Climbing Perch to show accessory respiratory organ; F, normal and G, inflated porcupine fish. (A and E, after Cuvier; B, F and G, after Günther; C, D, after Baskett.)

**Sub-Order XII. Pediculati** (five families).

These are the Anglers, Bathymal Sea-Devils, etc. (Fig. 371.)

**Sub-Order XIII. Plectognathi** (seven families).

These include the file-fishes, trunk-fishes, puffers, porcupine fishes and sun-fishes. (Fig. 371.)

**Sub-Class III. Dipneusti (Dipnoi).** The Lung-Fishes. (Fig. 372.)  
(Two extinct and two living families.)

These include the **Neoceratodus**, **Protopterus** and **Lepidosiren**.

The skeleton of lung-fishes is largely cartilaginous, but there is a tendency toward ossification. The swim-bladder serves as lungs. The very young individuals have long feather-like external gills.

#### Appendix to the True Fishes.

- I. **Palaeospondylidae** (one family between cyclostomes and fishes).
- II. **Ostracodermi** (three orders of eight families, mostly armored fishes).
- III. **Antiarchi** (one family of mailed fishes).
- IV. **Arthrodira** (one family of mailed fishes).

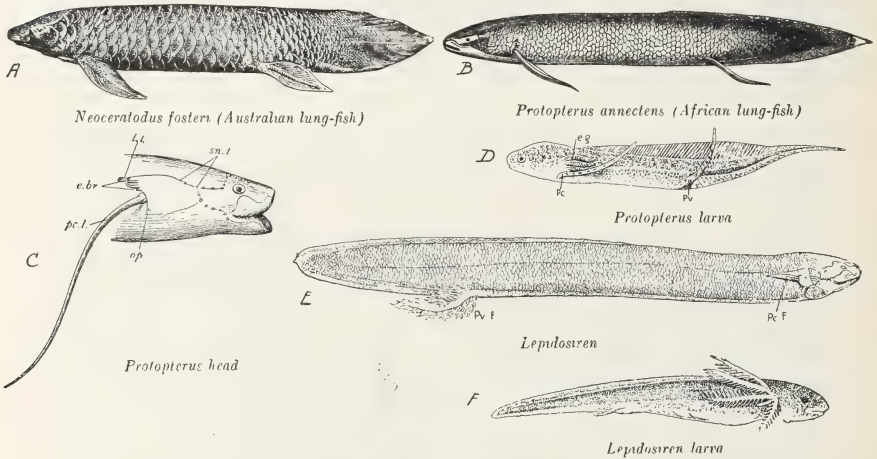


Fig. 372. Dipneusti.

In C, *sn.t.*, sensory tubes; *l.l.*, lateral line; *e.br.*, external gills; *pc.l.*, pectoral fin; *op.*, operculum. In D and E, *eg.*, external gills; *pc.*, pectoral fin; *Pv.*, pelvic fin. (A, after Günther; B, after Claus; C, after W. N. Parker; D, after Budgett; E and F, after Graham Kerr.)

It is well to note that 172 families of the 226 families of true fishes are members of the order **Teleostei**.

Of the **Elasmobranchii** there are 23 families now in existence and nine extinct.

The **ganoids** and **dipnoi** number 22 families.

#### Amphibia.

Contrasted with fishes, the amphibia have **pentadactyl appendages**, while contrasted with reptiles, they possess **double occipital condyles**. There are external gills in the larvae, though these do not always persist. The adults breathe by lungs. The heart consists of two auricles, one ventricle, a conus arteriosus, and a sinus venosus.

#### Sub-Class I. Stegocephali.

These are the extinct amphibia, many of which attained considerable size.

**Sub-Class II. Lissamphibia.** (About 1,000 species, nearly 900 of which are frogs and toads. Figs. 315, 376.)

**Order I. Apoda (Gymnophiona)** Limbless Amphibia. (Fig. 373.)

These are also called **caecilians** and sometimes "blind-worms." They are without limbs or limb-girdles. They burrow in the earth and are found in warm climes. The cranium is like that of the reptile in outward appearance, but the bones which constitute it are the same as those which go to form any amphibian cranium. The skin is smooth and slimy with many ring-like folds. There are as many as 200 to 300 vertebrae in some species. The eyes are rudimentary and probably functionless. Between eye and nose, a feeling organ protrudes which serves to guide the animal. Some are oviparous, while others are viviparous.

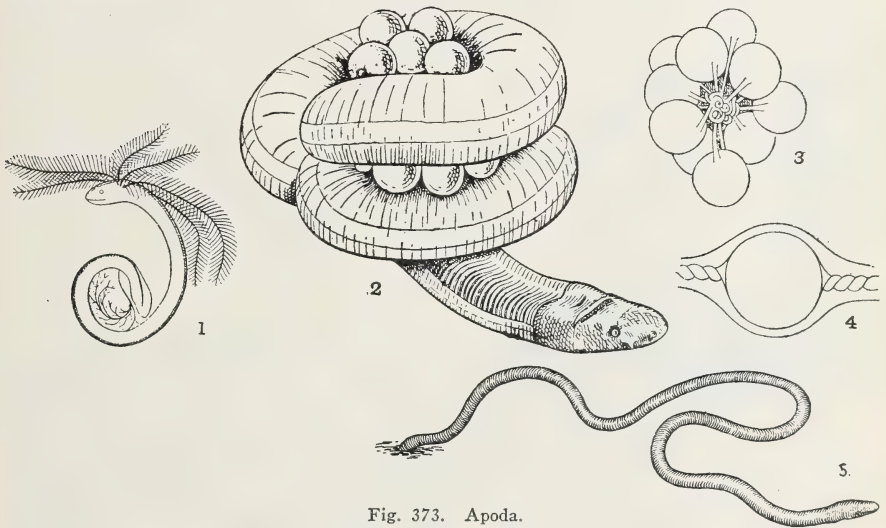


Fig. 373. Apoda.

*Ichthyophis glutinosa*. 1, nearly ripe embryo, with gills tail-fin, and with considerable amount of yolk; 2, a female guarding her eggs, coiled up in an underground hole; 3, a group of newly laid eggs; 4, a single egg, enlarged and schematised to show the twisted albuminous strings or chalazae inside the outer membrane, which surrounds the white of the egg. 5. *Caecilia*, emerging from burrow. (After F. and F. Sarasin.)

**Order II. Urodela (Tailed Amphibia).** (Figs. 315, 374.)

These are the mud-puppies (*Necturus*), salamanders, newts, and efts. Many authors call all urodeles with adult external gills, **Perenni-branchiata**, though the following grouping is the more common:

**Family I. Amphiumidae** (Fig. 374).

This family is without external gills in the adult stage. There are only two genera, **Cryptobranchus** and **Amphiuma** (Fig. 374).

**Cryptobranchus allegheniensis** (Fig. 374), is the well-known "hell-bender" of the Eastern United States.

**Cryptobranchus japonicus** is the giant salamander of Japan.

**Amphiuma** (Fig. 374) has only one species which ranges from Carolina to Mississippi in our Southeastern States. This is known as **Amphiuma means**, and is eel-shaped with much reduced limbs and a small pair of inconspicuous gill-clefts guarded by skin-flaps. Some of these animals are three feet in length, living in swamps and muddy water. The female protects the eggs by coiling about them.

**Family II. Salamandridae. (Salamander and Newts.)** (Fig. 374.)

These animals have no gills in the adult stage. Practically three-fourths of all tailed amphibia belong to this family.

The most common type is the **Desmognathus fuscus** (Fig. 374). The female coils about the eggs when laid. The young, after hatching, look quite like adult forms.

**Amblystoma tigrinum** or "tiger salamander" (Fig. 374) is very common in North America. It has large yellow spots which may merge into broad stripes or bands. The ground color is black. It may be

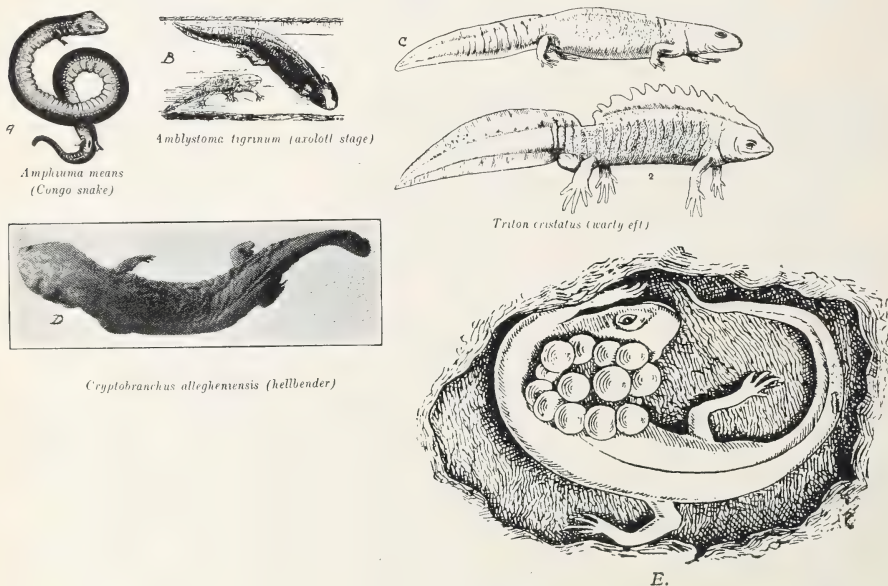


Fig. 374. Salamandridae.

In C, 1, Female; 2, Male at the breeding season with well-developed frills. E, *Desmognathus fuscus* (American newt). Female with eggs in underground hole. (A, after Molder; B, from Cambridge Natural History; C, after Gadow, E, after Wilder.)

found in damp places under stones and logs, or even in cellars of houses. For various reasons, it is one of the classic forms used in the laboratory. One laboratory value is that it is an animal which becomes sexually mature while still in the larval stage, a condition called **paedogenesis** or **neoteny**.

Another very interesting fact is brought out in the life of the larval forms of **Amblystoma**. The larva itself is called **Axolotl**, and was formerly considered to be a fully adult form. It is quite common near

Mexico City. However, when some of the **Axolotls** were taken to Paris, and kept in aquaria, they metamorphosed into regular, full-fledged **Amblystomas**. Not only this, but some of them could be made to revert back to the larval **Axolotl** form.

**Salamander maculosa**, commonly called the "spotted" or "fire salamander" is the most common of the European salamanders.

**Salamandra atra** is much darker than **S. maculosa** and is found in the Alps at altitudes from 2,000 to 9,000 feet. This animal is interesting in that it produces only two young at a time, which, while still in the uterus, feed upon the surrounding eggs and pass through their entire metamorphosis before being born.

Kammerer claims that **S. atra** will change to **S. maculosa** if brought to lowland waters and then after being kept there for several generations, and later returned to the higher altitudes, they will retain the breeding habits acquired as the lowland type. This fact has led some authors to insist that here is a case of acquired characteristics being inherited.

**Diemictylus viridescens** is the "vermilion spotted eft" or newt. It takes several years to reach the adult form. For three years it lives in water and has external gills. During this time it is green in color. Upon leaving the water, it becomes yellow with vermilion spots, and at the breeding season returns to water and again becomes green.

**Triton cristatus** (Fig. 374) is the "crested newt." The male has a decided crest during the breeding season.

**Family III. Proteidae.** (The Mud-Puppies), Fig. 375.)

These have **three pairs of fringed external gills** throughout life, and some authors call them **perennibranchii**.

There are only three genera, with a single species each. Two of these genera occur in America and one in Europe.



Fig. 375. Proteidae and Sirenidae.

(After Chapin and Rettger.)

**Necturus maculatus** is the common American "mud-puppy." It is assumed that this may be an animal which has remained in the larval stage.



### Sub-Order II. Phaneroglossa.

These are the frogs and toads with tongues. There are seven families.

The best known of these families are the **Bufonidae**, which are the common toads, and the **Ranidae**, the "true frogs."

There is a peculiar species of toads in France and Switzerland called **Alytes obstetricans** (Fig. 376), in which the male takes the eggs when laid and wraps them around his hind legs, after which he deposits them in a hole in the ground. These eggs are then moistened by him with dew and taken out occasionally in the water. When the eggs are ready for hatching, he takes them all to the water and remains with them until hatching is complete.

### Class Reptilia.

There are four orders of living reptiles. These are cold-blooded vertebrates, breathing by means of lungs throughout their life cycle. **Lizards**, **snakes**, **crocodilians**, and **turtles** come under the heading of **Reptilia**.

The fossil records of the past show that the four living orders are but a small portion of the variations within this class, which have continued their existence.

In the **Mesozoic era** (Fig. 245, Vol. I), commonly called the "age of **Reptiles**," there have been found many skeleton-remains of immensely large lizard-like animals. In fact, the name given to the largest of these animals of the past is **Dinosaur** which means "terrible lizard."



*Sphenodon punctatum*

Fig. 377. Reptilia.

(*Sphenodon* is considered the most primitive type of living reptiles.) (After Gadow.)

There were many flying reptiles at that time, while **Plesiosaurs** lived in the water and had long paddles for swimming instead of legs.

Reptiles with wings are called **pterosaurs**. Some of their fossil remains show these animals to have been twenty feet from tip to tip of wings when spread. It is assumed that these animals so overspecialized various parts of their body that, when great climatic and earth-changes came about, they could not cope with the new conditions. It has also been suggested that the eggs of many of these great animals may have been used for food by very small mammals, which caused the largest of all beasts to die out entirely.

The reptile most closely resembling extinct forms is thought to be **Sphenodon** (Fig. 377). It is confined to a few small islands off the coast of New Zealand and is hunted and eaten by the Maoris. It is also called "tuatara" and lives in burrows. Externally it looks like a lizard, though skeleton and viscera are quite unlike those of other living lizards.

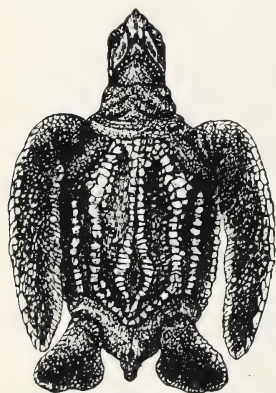
### Order Chelonia. (Turtles and Tortoises.)

These have a bony covering and toothless jaws. The covering consists of a dorsal or upper portion called a **carapace**, and a ventral **plastron**. These plates are soft in very young animals. The surface is covered with horny shields which Gadow believes to be phylogenetically older than the underlying bony plates. These latter do not correspond with the former in either number or position.

There are two sub-orders.

#### Sub-Order I. Athecae.

These are without a true carapace. There is only one living representative of this type, namely the **Leather-back Turtle**, known as **Dermochelys (sphargis) coriacea**. (Fig. 378.) Instead of the regular carapace, there are five dorsal, five ventral, and two lateral dermal plates. The tail is rudimentary and the limbs are large flipper-like paddles. Only large and very small specimens have ever been found. It is not known where they live between these stages.



*Sphargis coriacea*  
(leather-back turtle)

Fig. 378.

The only chelonian without a true carapace. (From Gadow.)

#### Sub-Order II. Thecophora.

These are the true turtles (Fig. 379) which are divided into two groupings. The first group is known as **Cryptodira** to which most turtles of the northern hemisphere belong. The head is retractile, and the pelvis is not fused to the shell. In Division II are the **Pleurodira**, representing a large group of the southern hemisphere. These do not retract the head but bend it sideways under the shell. The pelvis is fused to the shell.

The more commonly known American turtles belong to Division **Cryptodira**. The snapping turtles are members of the family **Chelydridae**. The skunk or musk-turtle is a member of the family **Cinosternidae**, and the common pond tortoises are members of the family **Testudinidae**. The "tortoise-shell" turtle belongs to those commonly called "sea-turtles" and is a member of the family **Chelonidae**.

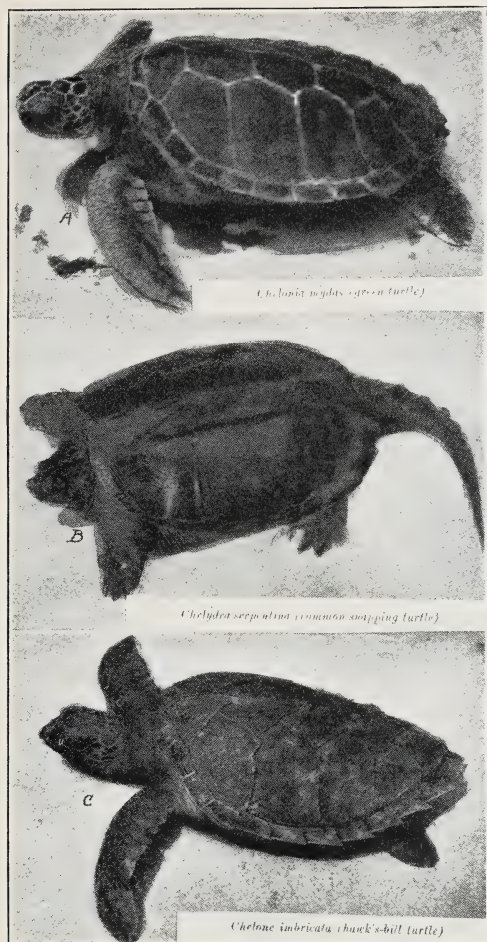


Fig. 379. Chelonia.

A, grows to weigh 800 pounds; B, 40 pounds C, smallest of marine turtles. This latter is the tortoise-shell turtle. (After Ditmars.)

## Order Crocodilia.

**Crocodilia** are characterized by well-developed limbs, long tail, fixed quadrate bone, and teeth fixed separately in alveoli. The various extinct forms, however, do not have all these characteristics.

There are only two families of **Crocodilia** (Fig. 380).

### Family I. Gavialidae.

There is only one living species of this family. It is called **Gavialis gangeticus**. It is found in the River Ganges and other large rivers of India.

### Family II. Crocodylidae.

This family includes both old and new world crocodiles and alligators. The latter animals do not grow so large as the crocodiles. The alligator is distinguished from the crocodile by having a broad, rounded snout.

## Order Sauria. (Squamata.)

These are the lizards and snakes. Their main differentiating characteristics are a movable quadrate bone which permits of a wide mouth-opening, a transverse cloacal aperture, and double copulatory organs.

## Division I. Lacertilia. (Lizards.)

While normally the ordinary forms of lizards are scaly and have four well-developed legs, there are many species which do not have these characteristics. This latter type appear quite like snakes, but the bones of the skull always serve to distinguish them. Then, too, the lizards have no elastic ligament between the two halves of the lower jaw as snakes have.



Fig. 380.  
Crocodilia. (After Baskett and Ditmars.)

There are three sub-orders (Fig. 381).

#### Sub-Order I. Geckones.

These are the primitive types having amphicoelous vertebrae (Fig. 404), and no bony temporal arches. They have dilated clavicles, separate parietals, eyes with movable lids, and a broad, fleshy, protrusible tongue, which is nicked at the end. The animals are usually harmless. The tail is loosely articulated and comes off when seized, although a new one grows quite readily.

#### Sub-Order II. Lacertae.

Most modern lizards belong to this group. Their vertebrae are procoelous and solid. The ventral portions of the clavicle are not dilated.

There are **cursorial types**, **arboreal types**, **volant types**, an **aquatic type**, a **fossorial type**, and an **ant-eating type**, so-called from their varying modes of life.

The Gila Monster (*Heloderma horridum*) of our southwestern states is the only poisonous lizard known, while the **monitor** (*Varanus salvator*) grows to the greatest length, something like seven feet or more.

#### Sub-Order III. Chamaeleontes (Chameleons). (Fig. 382.)

These animals are the ones so well known on account of their ability to change color and the enormously long tongue by which they readily catch insects at a distance of some seven inches.

Chameleons are highly specialized. The body is laterally compressed, the tail is prehensile, and the toes are parted in the middle so as to be used for grasping. They are found mostly in Madagascar. One species is found in southern Europe.

#### Division II. Ophidia (Snakes).

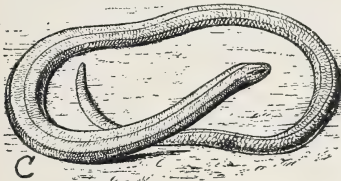
Snakes are really **Sauria**, or **Squamata**, in which the right and left halves of the lower jaw are connected with an elastic ligament which permits the mouth to stretch greatly. They are usually limbless or have



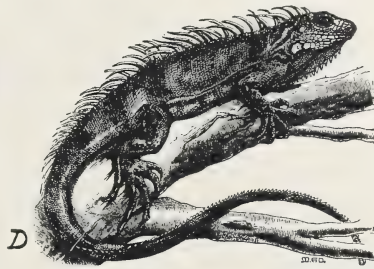
*Hemidactylus turicus*  
and *Tarentola mauritanica* (geckones)



*Heloderma* (Gila monster)



*Anguis fragilis* (limbless lizard)



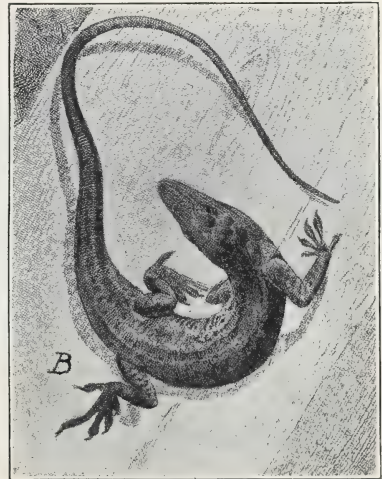
*Iguana tuberculata* (common iguana)

Fig. 381. Lacertilia.

(A and D, after Gadow; B, after Ditmars; C, after Shipley and MacBride.)



*Chamaeleon vulgaris*



*Anolis principalis* (American chameleon)

Fig. 382. Chamaeleontes.

(A, after Gadow; B, Ditmars.)

rudimentary limbs under the skin as has the python. The eyes are without eyelids.

### Class V. Aves. (Birds.)

These are closely related to the reptiles. In fact, reptiles and birds are often grouped together as **Sauropsida**. They have a single occipital condyle as do the reptiles. The heart of birds is, however, divided into right and left halves. Birds are warm-blooded. There is a fusion of the bones of the manus and there is the formation of a tibio-tarsus and tarso-metatarsus (intratarsal joint). Feathers cover the body.

Birds are commonly divided into: **Ratitae**, or "running birds," such as the ostrich, rheas, cassowaries, etc., whose sternum lacks a **furcula** (wish-bone) and a **keel** (Fig. 418); and the **Carinatae**, or the "flying birds." These latter have the sternum keeled and the clavicles are united to form the furcula.

There are two extinct groups which had teeth.

### Class VI. Mammalia.

These are warm-blooded animals, having a covering of hair, two occipital condyles, and milk-glands in the female.

Mammals are divided into two sub-classes.

**Sub-Class I. Prototheria**, or egg-laying mammals.

**Order I. Monotremata**, which consists of two families (Fig. 383).

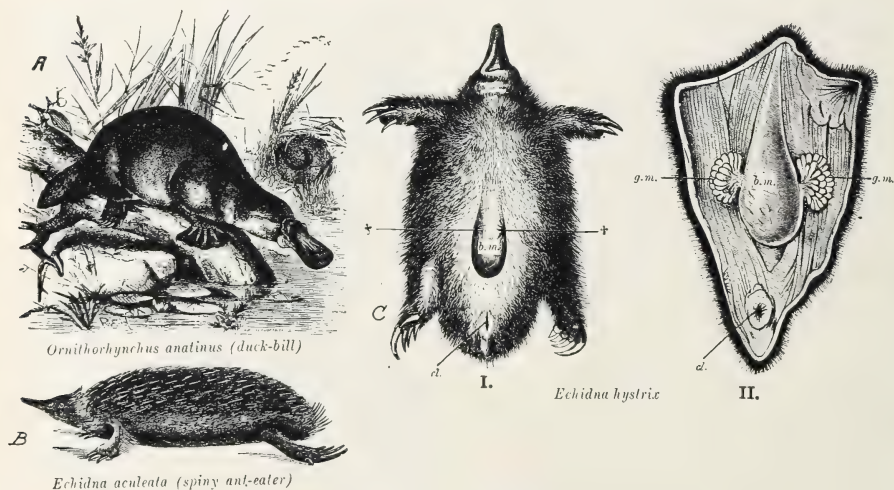


Fig. 383. Monotremata.

C. *Echidna hystrix*. I, lower surface of brooding female; II, dissection showing a dorsal view of the marsupium and mammary glands; † †, the two tufts of hair projecting from the mammary pouches from which the secretion flows; bm., brood-pouch or marsupium; cl, cloaca; g.m., groups of mammary glands. (A, after Shipley and MacBride; B, after Claus; C, after Haake.)

**Family I. Ornithorhynchidae.** (The duck-bill of Australia.)

There is **no corpus callosum** (Fig. 471), and the brain is the most primitive of all living mammals.

The eggs, two or three in number, and covered with a hard shell, are reptilian in form and are laid in a nest of grasses. The heat of the mother's body hatches them.

**Family II. Echidnidae.**

These are the Australian Ant-Eaters. There is a temporary marsupial pouch. Only one egg, about half an inch long, is laid at a time and placed in the marsupial pouch by the mouth of the mother. Here the young hatch in a very immature condition, the mother being obliged to remove the egg-shell after the young has come forth. The young **Echidna** obtains its food by licking the milk-like secretion exuding from the hairs in the pouch.

**Sub-Class II. Eutheria.**

These are the viviparous mammals which are divided into two divisions:

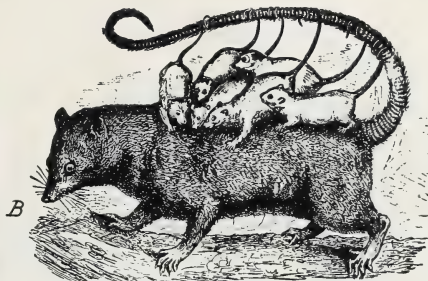
**Division I. Didelphia (Metatheria).** (Fig. 384.)

These are the marsupials.

**Order I. Marsupialia.** Mammals having a pouch to carry their young which are born in a rather immature condition. There is usually



*Petrogale xanthopus* (rock wallaby  
with young in pouch)



*Didelphys dorsigera* (South American opossum)

(A, after Vogt Specht; B, after Nicholson.)

Fig. 384. Didelphia.

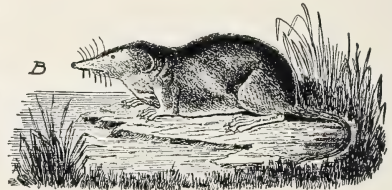
no placenta. Australia furnishes us with most **Marsupialia**, such as the kangaroo, wombat, phalangerer, pouched mole, and many other forms. The opossum is the only example in America.

## Division II. Monodelphia. (Placental Mammals.)

The young are never carried in a pouch, but a true placenta nourishes the unborn foetus.



*Scalops aquaticus* (common mole)



*Sorex vulgaris* (common shrew)

Fig. 385. Insectivora.

(After Coues.)

The placental animals are divided into the following sections: Unguiculates, Primates, Ungulates, and Cetacea.

### Section A, Unguiculates. (Clawed animals.)

Order I. Insectivora, such as moles, shrews, and hedgehogs (Fig. 385).

Order II. Chiroptera, such as bats (Fig. 386).

Order III. Carnivora, possess sharp teeth and claws.

Under this heading come the cat (**Felidae**) and dog (**Canidae**) families, for example, and many others.



*Xanthorpyia collaris* (bat)

Fig. 386. Chiroptera.

(After Sclater.)

Order IV. Rodentia are the gnawing animals. Rabbits, guinea pigs (**Cavia**), rats, mice, squirrels, etc., come under this heading.

Order V. Edentata. This name means toothless, but the animals, with the exception of the ant-eaters, belonging to this group do possess teeth. Different authors classify the **Edentata** in various ways. The animals usually coming within this group are sloths, ant-eaters, and armadillos. (Fig. 387.)

Section B, Primates. (Mammals with nails.)

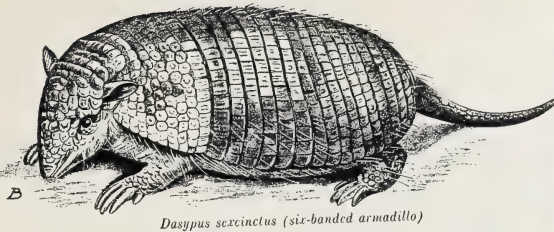


Fig. 387. Edentata.

(A and B, after Vogt and Specht; C, from Proc. Zool. Soc. 1871.)

**Order VI. Primates.** Mostly tree-inhabiting animals, with nails on fingers and toes instead of claws or hoofs. The monkeys, which are to be included under this heading, are divided into **Platyrrhine** (broad-nostril) and **Catarrhine** (narrow-nostril) groups. The former are peculiar to the New World and the latter to the Old World. The higher apes belong to the Old World group. New World monkeys have a prehensile tail (Fig. 388) while no Old World monkeys possess



Fig. 388.

Note the prehensile tail so characteristic of New World Monkeys.

this. In the **anthropoid**, or manlike, apes (**Simiidae**), (Fig. 389), there is no tail at all.

**Section C, Ungulates.** (Hoofed animals.)

**Order VII. Artiodactyla** (even-toed ungulates), are pigs (**Suidae**), deer (**Cervidae**), giraffes (**Giraffidae**), cattle, sheep, goats (**Bovidae**).

**Artiodactyla** are all terrestrial or mud-inhabiting animals, usually of large size, having hoofs on two or four toes. Their stomachs usually have several chambers and are peculiarly adapted for an herbivorous diet.

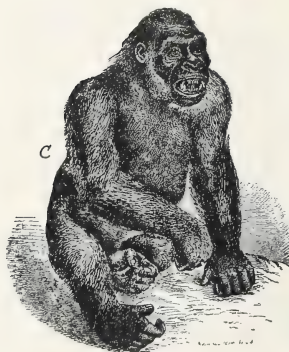
Artiodactyla are often divided into two groups:



*Hylobates entelloides*  
(dun-colored gibbon)



*Pan (Anthropopithecus)*  
*troglodytes* (chimpanzee)



*Gorilla engena*



*Simia satyrus* (orang-utan)

Fig. 389. Simiidae.

(A and B, after Flower and Lydekker; C, after Vogt and Specht; D, after Shipley and MacBride.)

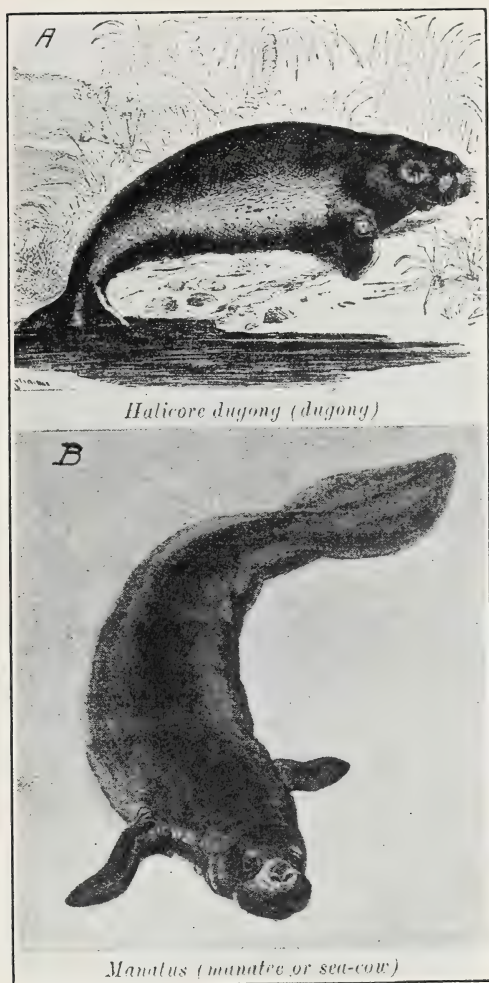


Fig. 390. Sirenia.

(A, from Brehm; B, from Ingersoll.)

**Group I. Suina.** (Swine-like.)

All the swine family come under this heading, including the hippopotamus which is really an aquatic hog.

**Group II. Ruminantia.** (Ruminants.)

The animals belonging to this group swallow their food rapidly and later regurgitate it into the mouth for further chewing. Such animals are said to "chew a cud." Camels, llamas, antelopes, cows, giraffes, goats and sheep belong here.

**Order VIII. Perissodactyla.** (Odd toed ungulates.)

In this order, the animal walks on the middle digit of fore and hind feet. The following three families make up the entire order: **Equidae** (horses, asses, and zebras); **Tapiridae** (tapirs); and **Rhinocerotidae** (rhinoceroses).

**Order IX. Proboscidea.** (Elephants.)

**Order X. Sirenia.** (Sea-cows such as dugongs and manatees, Fig. 390.)

Aquatic offshoots of ungulate stock.



*Hyrax abyssinicus* (coney or hyraxes)

Fig. 391. Hyracoidea.

(From Lull after Brehm.)

**Order XI. Hyracoidea** (Conies, Fig. 391).

Short-eared, rodent-like, primitive ungulates, usually living among rocks, although some are tree-inhabiting.

**Section D. Cetacea** (Whales and dolphins, Fig. 392).

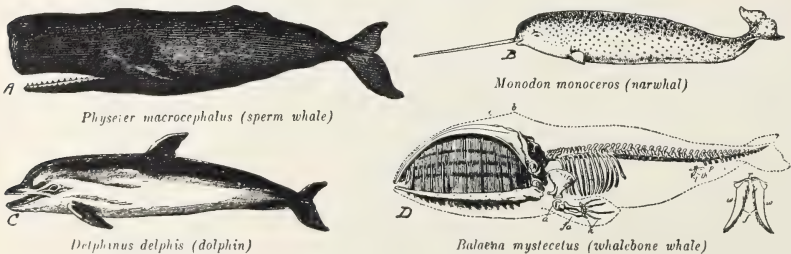


Fig. 392. Cetacea.

In D, *a*, upper arm; *b*, blow-hole; *fa*, forearm; *h*, hand; *p.th.l*, small remains of pelvis, thigh, and leg; *r*, roof of palate; *w.w.*, plates of whalebone; *f*, whalebone fringe. (A, after Flower and Lydekker; B, after Cuvier; C, after Sedgwick; D, after Holder.)

**Order XII. Odontoceti** (Toothed-whales).

Examples of these are: sperm-whales, narwhals, beaked whales, porpoises, and dolphins. They have teeth but no whale-bone. They possess a single nostril or "blow-hole," and some of the ribs are two-headed.

**Order XIII. Mysticoceti** (Whale-bone whales).

These are also called **baleen** whales.

For convenience sake the following terms are often used:

**Ichthyopsida.**

This is a name given to **Cyclostomes**, **Gnathostomes**, and **Amphibia** combined. The distinctive characteristics of the **Ichthyopsida** are that all animals belonging to this group breathe by means of gills at some period of their life's history. They are, therefore, **aquatic vertebrates**.

They are sometimes called **Anamniota** or **Anamnia**, because they do not develop an **amnion**, and **Anallantoida** because they do not develop an **allantois**.

**Sauropsida.**

This is the name given to **birds and reptiles** combined. The distinctive characteristics of the **Sauropsida** are that all animals belonging to this group breathe with lungs and never develop functional gills. They are, therefore, **terrestrial vertebrates**. **Sauropsida**, together with the **Mammalia**, are called **Amniota** on account of their developing an **amnion**, and **Allantoida** on account of their developing an **allantois**.

**Tetrapoda.**

This is the collective name assigned to **all four limbed animals**, whether they are amphibians, reptiles, or mammals.

## CHAPTER XXI

### THE INTEGUMENT

**I**N examining an organism it is logical to first examine its external structure. It is thus the outer covering of the body which becomes our first object of study. In fishes we, therefore, study **scales**; in the frog and the human being, the **skin**; while on most mammals, **fur**; and on birds, **feathers**. Yet, whatever forms such external parts may assume, they are a **covering of the body**, and as such form what is called an **integument** ( ). **This term includes the skin, or cutis, and all the structures derived from it.** If an animal lives in water, the effect of water upon such covering must be considered; likewise, consideration must be given to whether an animal lives in a cold climate or in a warm, whether it lives in the air or burrows beneath the earth. All these things are bound to have modifying effects upon an animal's outer covering.

Microscopically the integument of vertebrates consists of **two layers**: (Fig. 393), an outer, **epidermis**, which is the remainder of the ectoderm after the nervous system has been separated from it, and a **deeper layer, the corium, or derma**, composed of **mesenchyme** which has been derived from the **somatic portion** of the **somite**. It is into this deeper structure that the nerves and blood vessels extend.

Accessory organs are developed in both layers, but may begin growth in one and extend through the other. In all cases, however, each element of the accessory organs has a very definite place of origin.

The **integumental glands** thus arise from the epidermis, though dipping down into the corium to receive a fibrous covering.

**Pigment** usually develops in the corium and often then migrates to the epidermis, although it does sometimes develop in the latter layer itself.

**Blood vessels** (except in the mucous membrane of the pharynx of lungless salamanders) develop in the corium.

**Sensory nerve endings** are quite freely distributed throughout the epidermis, but the more specialized forms remain in the corium, often pushed up into the epidermic zone in the form of papillae. The epidermis is thus a bloodless, protective covering with but slight sensitiveness. All the more delicate structures are found in the lower layer or dermis.

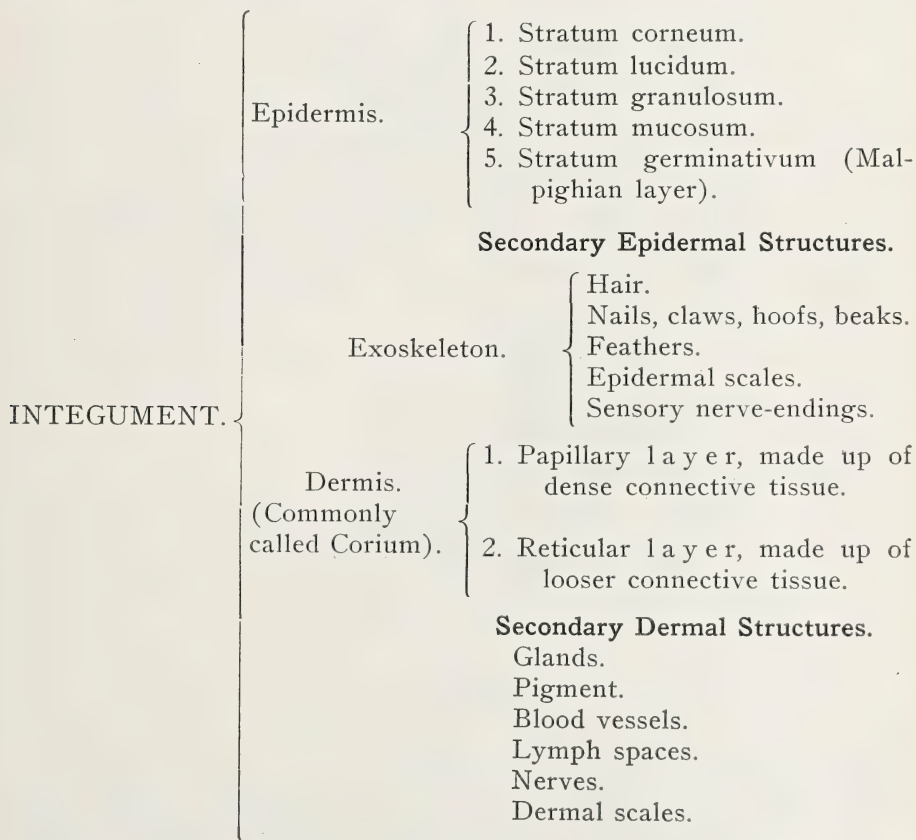
Both skin layers have the power to form hard parts, known as **exoskeleton**.

**True bone**, for example, develops from the corium, while **horn** and **enamel** originate in the epidermis.

Horny structures, such as hairs or feathers (Fig. 394), are formed

from the epidermis alone but dip down into the richly vascular corium to obtain nourishment. The dermal scutes of ganoids and the dermal bones of higher forms arise entirely within the corium. Teeth are composite structures composed of **dentine**, a hard sort of bone from the corium, overlaid with **enamel** from the epidermis.

It is important that one does not confuse the term integument with mere portions of the integument; for example, the **epidermis** is merely an **outer histologic layer**. The **ectoderm** is merely **one of the germ layers** from which both integument and the nervous system arise. The **skin alone** on such animals as have feathers, scales or fur, likewise **would not be the integument**, but **both skin and its immediate outer covering** would constitute such protective substance. The following schematic arrangement in man is that commonly used in medicine:



**Note:** The exoskeleton of vertebrates consists of **bone**, **horn**, and **enamel**.

**Bone** originates in the corium (**mesodermal**).

**Horn** and **Enamel** originate in the epidermis (**ectodermal**).

In comparative anatomy, the epidermis in turn is divided into two layers, the lower one being known as the **Malpighian layer** or **stratum germinativum** (Fig. 393). Usually this layer rests on the **corium** and is nourished by the fluids from the corium. The cells, therefore, grow outward as they divide to form a second or outer layer, the **stratum corneum**. These outer cells come in contact with the surrounding media and are worn away almost as fast as new ones are added from

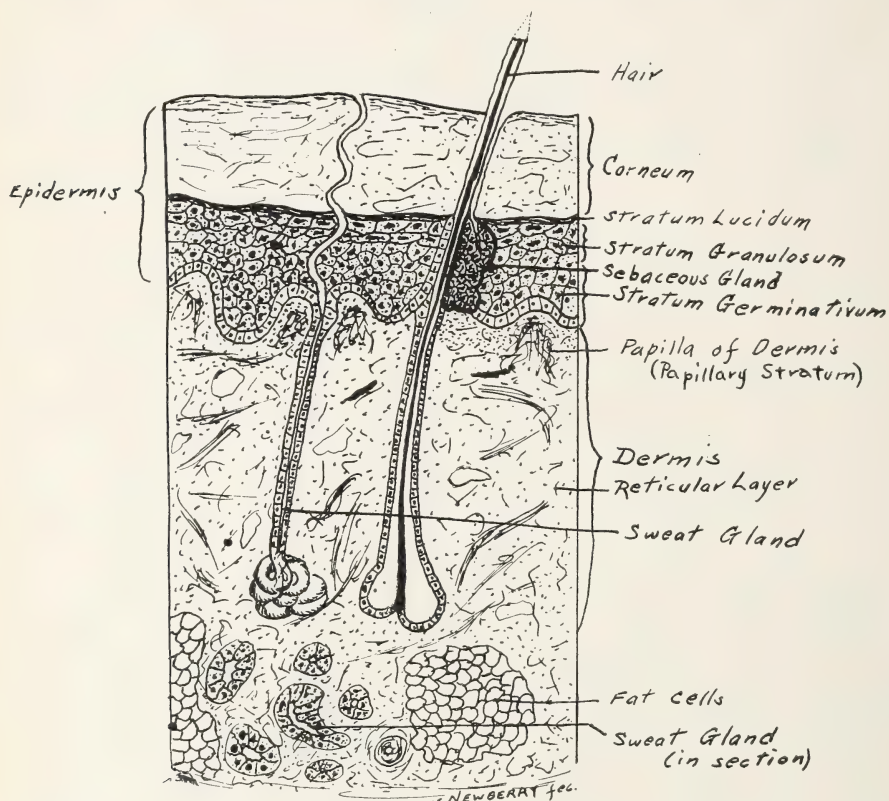


Fig. 393.

Diagram of a section through the skin of a mammal to show various layers, hair, and sebaceous and sweat glands.

below. If these outer cells come off in large sheets, we find such a condition as that of a snake shedding its skin.

In land animals, the first layer of cells budding off from the Malpighian stratum seems to be a continuous sheet which is likely to be shed as a whole. This is called the **periderm** (Fig. 395). Older books call this the **epitrichium**, but as this word means "above the hair" it is not accurate when it refers to reptiles and birds which have no hair.

The Malpighian layer is that in and from which the **glands of the**

skin are formed, while the corresponding part of the ectoderm contributes to such **sensory structures** as the nose and ear.

The **hair, nails, claws, feathers**, and other **outgrowths of the cutis** come from the **epidermis** (Figs. 393, 394). Land animals usually have a thicker epidermis than those which live in water. The latter keep the outer portion of the body constantly moist and so show less of the hardened, or horny, consistency which is found in animals living in the air. The **corium** lies **directly beneath the epidermis** and is connected by means of a loose layer of connective tissue with the deeper structures. The corium itself is a mass of fibrous connective tissue in which there is an intermingling of **elastic tissue, blood vessels, nerves, smooth muscle fibers**, etc. It is much thicker in mammals than in the lower vertebrates.

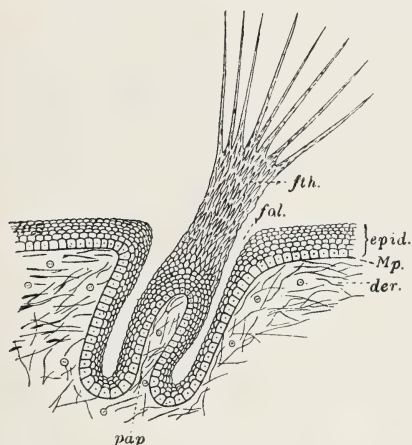


Fig. 394.

A diagram of a developing feather, highly magnified. *der.*, Dermis; *epi.*, epidermis; *fol.*, follicle; *fth.*, feather; *Mp.*, Malpighian layer of epidermis; *pap.*, papilla by the growth of whose epidermis the feather is formed. (From Shipley and MacBride.)

It is the corium which is commonly known as **leather**. In both epidermis and corium pigment cells may be found. These are mesenchyme cells loaded with pigment. They are frequently under the control of the nervous (sympathetic) system and can be altered in shape (**chromatophores**), thus producing color changes, which as in the **chameleons**, may be very marked.

If the epidermis becomes **cornified**, scales are produced. This takes place by certain cells in both corium and epidermis beginning to multiply in certain definite regions. These thickenings become future scales by the

**stratum corneum** turning into a horny material. In snakes and lizards these scales, together with all of the stratum corneum (even the covering of the eye), are periodically **moulted**, the separation taking place at the surface of the stratum Malpighii. In turtles and alligators there is a gradual wearing away of the surface.

**Claws, hoofs, and nails** are closely allied in their manner of growth to scales (Fig. 396). In fact, a claw is formed by two scales. The dorsal one is called the **unguis**, and the ventral the **sub-unguis**. The dorsal scale grows continually from a root and in mammals is forced over its bed. The unguis is curved both transversally and longitudinally, while the sub-unguis forms its lower surface.

In the human nail, the unguis is nearly flat in both directions, and the sub-unguis is reduced to a narrow plate just beneath the tip of the

nail. In the hoof, the unguis is rolled around the tip of the toe, while the sub-unguis forms the "sole" inside it. The "frog" is the reduced ball of the toe which projects into the hoof from behind.

The comparisons in this part of the work will be between **fishes, amphibians, reptiles, birds, and mammals**, as these represent the great **type-forms** of vertebrates.

## FISHES

The life in water makes horny cornification very rare. The epidermis of fishes is, therefore, soft. "Pearl organs," however, appear during the breeding season in some teleosts. Glands are quite abundant, the secretion furnishing the slime on the surface. Some groups of fishes also possess poison glands, usually in close relation to the spines of the fins. The elasmobranchs have large **pterygopodial glands** in the "claspers" of the males. The purpose of these glands is not known.

**Photophores** are some of the most interesting and striking of all epidermal organs. They are usually found in elasmobranchs and teleosts

from the deep seas, where sunlight does not penetrate.

In reality, they are formed very much like an eye by the cells of the Malpighian layer dipping into the corium. Here they are cut off from their origin, forming a deeper glandular layer. The outer rounded body is called the lens. The corium then forms a reflecting layer, which in turn is enclosed by a coat of pigment.

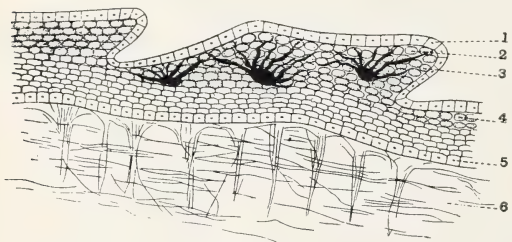


Fig. 395.

Section through the scale of a Lizard. 1. Peridermal layer. 2. Heavily cornified cells forming the scale. 3. Pigment cell. 4. Ordinary cells of horny layer. 5. Innermost Malpighian layer. 6. Dermis. (After Shipley and MacBride.)

In the myxinoids many thread-cells in little pockets are located in various portions of the skin. Each of these cells contains a long thread which is discharged upon stimulation, the threads forming a network in which the mucus secreted by the ordinary gland cells is entangled. Artificial pearls are made from "essence of pearl," which is formed in the fibrous tissue of the corium of some fishes.

## AMPHIBIA

The interesting point about these animals is that during the early larval stage the epidermis is often ciliated and two cells in thickness. There are numerous mucus and poison glands, sometimes enlargements of the neck called "parotid glands." These occur on the **anura**, and there is likewise a gland on the back near the base of the tail. It will be remembered that the large lymph spaces under the skin of the frog make

it possible to remove that animal's skin quite readily. As amphibians and the lungless salamanders respire largely by the skin, the corium is richly supplied with blood vessels, which, at the time of the metamorphosis of anura, penetrate into the epidermis. It is at this time that the lungs are not yet functioning, and the gills are being absorbed. The stratum corneum is shed periodically, either as a whole, as in urodeles, or in patches. The "warts" of toads are partially cornifications of the epidermis. A similar hardening of the skin at the ends of the toes results in claws.

## REPTILES

All these have horny scales and sometimes bony plates, though some of the fossil groups have a naked skin.

Glands are rare, though some "turtles have scent glands beneath the lower jaw along the line between carapace and plastron; snakes and crocodilians have them connected with the cloaca, while the latter have others, of unknown function, between the first and second rows of plates along the back, as well as protrusible musk glands on the lower jaw."

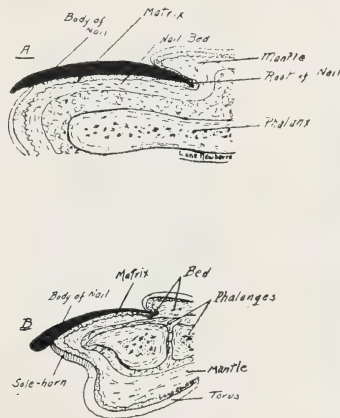


Fig. 396.

Comparison of human finger nail (A) and hoof of horse (B).

These latter are not true glands, as they produce no secretion, but cast out the living cells. Color changes are not remarkable except in a few snakes and lizards. Claws are common on the toes.

The so-called "femoral pores" on the under surface of the legs of lizards are not true glands. They are epidermal structures composed of horny cells and possibly have a sexual function.

## BIRDS

The distinguishing characteristic of birds is that they possess feathers. Both layers of skin are quite thin. Both scales and feathers

are developed from the epidermis, although there are extremely few glands. Some birds, like the ostrich, possess no glands, though a great many species have the so-called **uropygial gland** at the base of the tail which pours out an oily secretion for dressing the feathers. In a few **rasores** (scratching birds), there are modified **sebaceous glands** near the ear. The scales on the legs, as well as the claws on the feet and sometimes on the wings, are often said to be derived from reptilian ancestors.

Feathers are closely related to scales. There are several kinds of feathers, conveniently grouped under three heads:

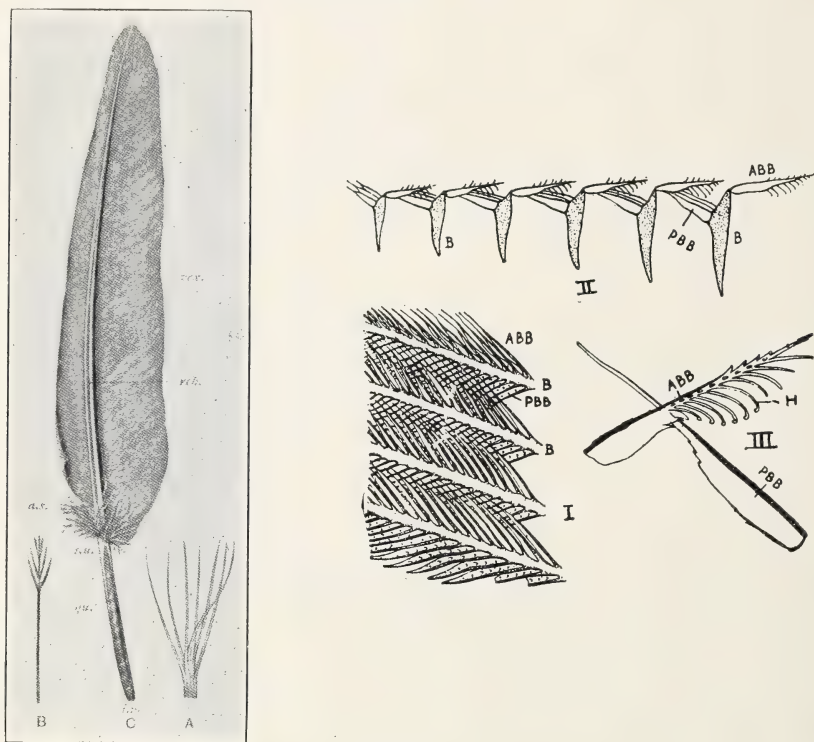


Fig. 397.

Feathers of a pigeon. *A*, Down feather; *B*, filoplume; *C*, quill feather. *a.s.*, Aftershaft; *i.u.*, inferior umbilicus; *q.u.*, quill or calamus; *r.ch.*, rhachis or shaft; *s.u.*, superior umbilicus; *vex.*, vexillum or vane. (After Borradaile.)  
*I*, *II*, *III*.—Parts of a feather. *I*, Four barbs (*B*) bearing anterior barbules (*ABB*) and posterior barbules (*PBB*); *II*, six barbs (*B*) in section showing interlocking of barbules; *III*, anterior barbule with barbicels (*H*). (After Nitzsch.)

- (1) **Filoplumes** (hairy feathers).
- (2) **Plumulae** (down feathers).
- (3) **Plumae** (contour feathers).

It is the **plumae** that have the typical form consisting of shaft and vane. (Fig. 397.) The base of the shaft is the hollow quill in which a small amount of loose pith is found. The shaft or **rhachis** is solid, and

a groove runs the length of its lower surface. This is the **umbilical groove**. The vane consists of lateral branches, or **barbs**, on either side, which have, in turn, still smaller side branches called **barbules**. These latter usually have small hooks at their sides and tips. These hooks interlock to give firmness and continuity to the whole vane. In down-feathers, where hooks are lacking, the barbs arise directly from the end of the quill, the barbs do not interlock, and no vane is formed. Hair-feathers consist of long slender shafts with a few terminal barbs.

**Archaeopteryx**, the oldest known fossil bird, had well developed contour feathers. In most birds, feathers are not equally distributed,

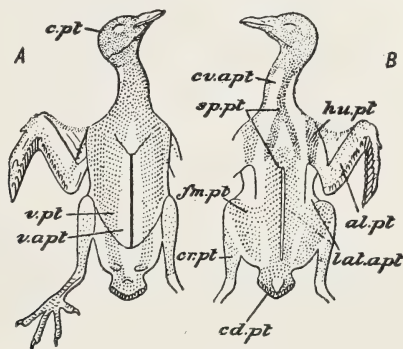


Fig. 398.

Feather tracts of the pigeon. *A*, ventral; *B*, dorsal. *al.pt*, alar pteryla or wing tract; *c.pt*, cephalic pteryla or head tract; *cd.pt*, caudal pteryla or tail tract; *cr.pt*, crural pteryla; *crapt*, cervical apterium or neck-space; *fm.pt*, femoral pteryla; *hu.pt*, humeral pteryla; *latapt*, lateral apterium; *sp.pt*, spinal pteryla; *vapt*, ventral apterium; *v.pt*, ventral pteryla. (From Parker and Haswell, after Nitzsch.)

but are gathered in tracts, known as **pterylae** (Fig. 398), and separated by **apteria**, or featherless regions, where there are but few down or hair feathers. These feather-tracts vary, however, in different groups of birds, but are used to a considerable extent in classification.

There is a great similarity in the method in which the integument develops in the different type forms we are studying (Fig. 394). For example: "A down-feather begins as a thickening of the corium, pushing the epidermis before it. By continued growth this forms a long, finger-like papilla projecting from the skin. The corium extends into the outgrowth, carrying blood-vessels with it, while an annular pit, the beginning of the feather follicle, forms around the base of the papilla. Next, the corium, or pulp of the distal part of the papilla, forms several longitudinal ridges which gradually increase in height, growing into the epidermis and pressing the Malpighian layer above them against the periderm. As a rule, the stratum corneum is divided distally into a number of slender rods arising from the base (quill), which at last are only

held together by the periderm. Then the pulp retracts, carrying with it the Malpighian layer. With the blood-supply removed, the epidermal parts dry rapidly, and the periderm ruptures, allowing the rods to separate, forming the down."

Up to a certain point, contour-feathers are quite like down-feathers in their development.

It is to be remembered that the dorsal and ventral sides of the feather **were the outside and inside of the stratum corneum of the papilla**. Scales of lizard skin show extreme similarity in their development to the feather just described (Fig. 395). Many smooth muscle fibers act to elevate the feathers in the corium of birds, and there are also tactile or sense organs. The colors of feathers depend partly upon red, yellow, orange, brown, and black pigment deposited in them, but the iridescent colors are due to interference spectra.

## MAMMALS

Mammals have a relatively thicker skin than other vertebrates (Fig. 393). There are many glands and considerable hair, except in a few orders such as the whales and sirenians. There are likewise horns and claws as well as scales, though the latter are not so conspicuous in the higher forms.

The corium is quite thick and is composed of irregular fibers interlaced with muscles, blood vessels, etc. Its outer surface often forms papillae or ridges, especially on the palms and soles. These ridges carry the epidermis with them. Several strata may usually be recognized under the epidermis, namely: a thick **Malpighian layer** at the base, then a thin **stratum lucidum** in which distinct cells cannot be recognized, and the **stratum corneum** on the outside. One or more other layers may be present. A cell must pass through all of these layers before it is worn from the surface of the skin.

## HAIR

It is important that the histological structure of a hair (Figs. 393, 394) be compared with that of a feather already described.

Scales are found in many orders, usually best developed on the tail and feet. They are rounded, quadrangular, or hexagonal, the square scales being arranged in rings around the part, the others in groups of five known as **quincunx**. These latter are closely similar to the scales of reptiles. It seems, from recent investigations, that there is a close relation between scales and hair, since in mammals with scales, hairs are usually arranged in groups of three or five behind each scale; and in those without scales, the hairs are also grouped in the same manner. In the early embryo, the hairs are arranged in longitudinal rows so that grouping seems to come later.

## GLANDS

These are of various kinds and types. The structural shapes and forms into which they may be grouped have already been studied in the frog and should be recalled, but we must also think of five divisions or groups, classified not according to structure, but according to function. Thus we have the following grouping:

(1) **Sweat** (tubular in shape), extending from the Malpighian layer down through the corium where they are coiled.

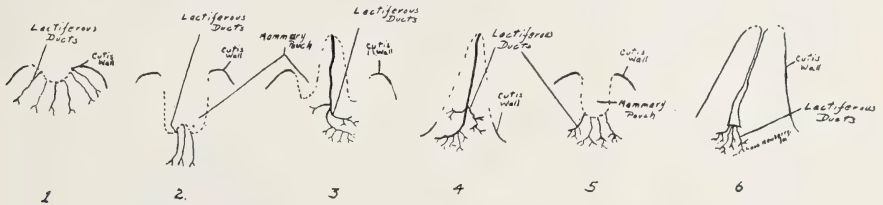


Fig. 399.

Schematic arrangement of varying types of mammary glands. 1, *Echidna*, primitive type; 2, *Halmaturus* (a genus of Kangaroo) forming pouch in lactation; 3, *Didelphys*, forming of nipple before lactation; 4, Same during lactation (quite like man); 5, Mammary pouch in cow embryo; 6, in adult cow. (After Max Weber.)

(2) **Sebaceous** (acinous in shape), connected with each hair (Fig. 393).

(3) **Mammary** (modified tubular glands) which produce milk (Fig. 399).

(4) **Tarsal** or **Meibomian** (modified sebaceous glands), in eyelid, producing oil to keep tears from overflowing (Fig. 400).

(5) **Anal** (acinous in form), commonly scent glands, secreting a substance either for sexual attraction or for protection (Fig. 400).

Glands are often also divided according to the method by which they furnish their secretions. First, **necrobiotic glands**, which burst when liberating their fluids. The individual gland is then destroyed. And, second, **vitaly secretory glands**, the secretions of which are poured through the walls of the gland while the gland itself remains functional for an indefinite period. In fact, this physiological distinction is often used to determine homologies when other methods cannot be used.

Each animal class seems to develop integumental glands in its own peculiar way. No definite and continuous history of gland development may be found throughout the various groups. Those animals living in the water, such as fish and amphibians, have glands that secrete protective substances which are often poisonous. The **Sauropsida** seldom have any integumental glands at all, and snakes have characteristic **cloacal glands** secreting a particularly nauseating substance. Certain turtles have so-called musk-glands, probably for sexual attraction. In some lizards there is a row of so-called glands (really femoral pores),

along the inner portion of the femora, that secrete a substance at breeding time which hardens into short spines or teeth. In birds there are only the **uropygial glands** in the caudal region, which furnish an oil for the feathers.

In mammals there are many and varying glands in the skin, but they may all be placed into two groups (Fig. 400), namely, the **sweat-glands**, which are vitally secretory and tubular, and the **acinous glands**, many of which are lobed and necrobiotic, although both originally arise in connection with the hair.

The secretion from the sweat glands is usually thin and watery,

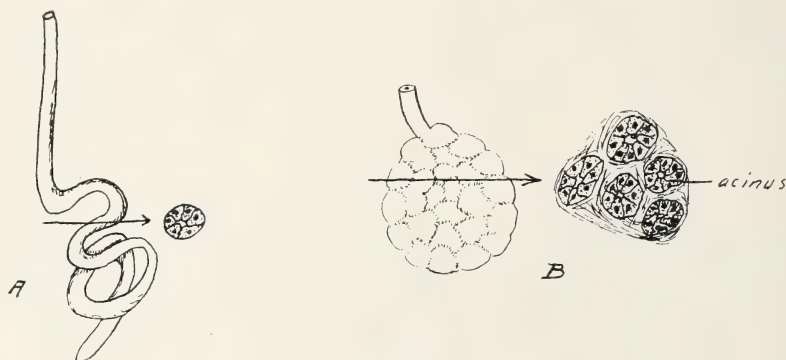


Fig. 400.

*A*, Sweat gland; *B*, Acinous gland. Complete gland and cross section. The cross section is cut at the level of the arrow. (Compare with Fig. 393.)

although it may vary from this to a thick viscous pinkish fluid, the so-called "blood-sweat" of the hippopotamus.

The sweat glands may be found almost anywhere on the entire body or they may be localized. Localization takes place most frequently in the paws or on the palms of the hand and soles of the foot. Here they serve to assist in grasping a given object more solidly.

A modification of these glands also furnishes the oily secretion of the ear.

It probably has been observed that in hot weather horses sweat quite profusely while dogs do not. This is due to the fact that horses have sweat glands in the skin while dogs have not, so that dogs can only obtain the same relief that other mammals obtain, during such weather, by opening their mouths and panting, as it is only in this way that the constantly accumulating moisture finds its way to a surface where evaporation then brings about a cooling. Muzzles should, therefore, always permit the opening of the mouth.

There are some races of men, such as the Fuegians, who likewise have few sweat glands.

The acinous glands furnish an oily secretion, apparently for the

original purpose of lubricating the hair, regardless of how far removed from this function such glands may ultimately come to be. These glands are called **sebaceous**. The **tarsal**, or **meibomian**, glands of the eyelids are practically hypertrophied sebaceous glands of the eyelashes. These meibomian glands pour out an oily secretion which lubricates the edge of the lids and prevents tears from overflowing. There are modified sebaceous glands in the various orifices of the body such as in the lips and about the anus.

Then there are groups of glands which are localized for quite specific functions, such as the anal-sacs of the skunk, which secrete a protective substance, and the sexually attractive glands, such as those of musk or civet. Musk is often used in the manufacture of perfumes.

Glands usually open as an elevation at a single place, known as a glandular area. The milk-glands of mammals are typical examples, but there are cases where there is a sinking of the area so that instead of the young taking a nipple in their mouths, the lips of the sunken area fit closely about the nose of the young and thus prevent the secretion from being lost. Such is the case in **Echidna** (Figs. 383, 399). In the opossum the nipple is really a sac like that in **Echidna**, but turned inside out.

It is a common observation that in many of the domesticated animals there is a row of nipples extending from axilla to the groin. In the embryo of many placental animals there is an entire ridge along which the mammary glands are to appear. In a short time there are suppressions at regular intervals, which leave protruding nipples. These nipples in turn become reduced and eventually become actual depressions.

The varying position of the nipples in different groups of animals is due to the retention of some of the nipples in a particular region and the suppression of the remaining ones along this lateral ridge, which, as mentioned, extends from axilla to groin.

It is of interest that the aquatic **Sirenia** (Fig. 390) have pectoral mammary glands. They bear but a single young at a time and nurse their offspring by standing erect in the water while clasping the young in their flippers. It is supposed that many of the mermaid stories had their origin from an observation of this animal nursing its young.

It is by no means uncommon to find animals (including man) having a peculiar arrangement of nipples on their bodies. Supernumerary nipples are termed **hyperthelism**, and supernumerary mammae are termed **hypermastism**. These supernumerary developments sometimes occur on the thigh and other parts of the body. They are considered **displacements** and **not reversions** if they occur in out-of-the-ordinary regions, and **reversions** if they occur in regions where they normally develop embryologically.

While rudimentary nipples occur in the male of placental mammals,

and may even prove to be functional in some instances, monotromes and marsupial males do not develop them at all.

## SCALES

As the dog-fish has what is called the **indifferent type of an exoskeleton**, it is this animal which forms the classic example for a preliminary study. Here we find imbricated rows of pointed scales (which merely means that one row of scales covers the intervals of the next row). (Fig. 401.) The scales of other fishes, as well as of reptiles, and even the feather papillae of birds, and the hair of mammals, are all arranged in a similar manner.

The scales of the dog-fish are said to be **placoid** (Fig. 401), which means that each has an approximately flat base from which a sharp-pointed cusp arises. This cusp is inclined in the direction of the free edge of the scale. When the scale is in place, the inclination is toward the posterior portion.

The scale itself consists of a core of dentine which is overlaid with enamel. In fact, the cusp is almost all enamel. The papilla from which nourishment comes to the scale lies beneath. In the embryo the scale forms between epidermis and corium, the dentine arising from the corium, and the enamel from the epidermis.

In the selachians there are several rows of pointed teeth arranged quite like the scales on the surface. These develop from the same layers and in the same manner as the scales, and consist of a similar structure, so they are assumed to be merely placoid scales modified by different usage.

All higher vertebrates inherit teeth. In birds and turtles they are supposed to have been secondarily lost.

Ganoids (Fig. 368) develop their scales (Fig. 401) from the corium alone, the epidermis playing no part. Consequently the ganoid scale is all dentine. Ganoid scales are shiny, which is the very meaning of the term "ganoid." They are usually rhomboidal in shape and do not possess a cusp. In the sturgeons (Fig. 368), the scales consolidate into large bony shields called **scutes**. The former **mailed** or **armoured fishes** merely carried this consolidation to great extremes, and the plates were continuous. In the sturgeons the plates are not continuous but are placed in rows along the back and sides so that there are large areas unprotected.

It is important to note at this point that in all ganoids (Polypterus, sturgeons, paddle-fishes, gar-pikes, and bow-fins, Fig. 368), the plates or scutes cover the entire head. The coming together of the edges forms sutures while the structures lying between the sutures are commonly called the **dermal bones** of the skull.

**Frontals, parietals, maxillaries, and squamosals** are found in all

higher groups, though the opercular and rostral series disappear entirely. Most of the orbital series also disappear, with the exception of the lacrimal. Then, too, there are the dermal bones of the mouth cavity, such as **vomers**, **palatines**, and **parabasal**, which are supposed to have

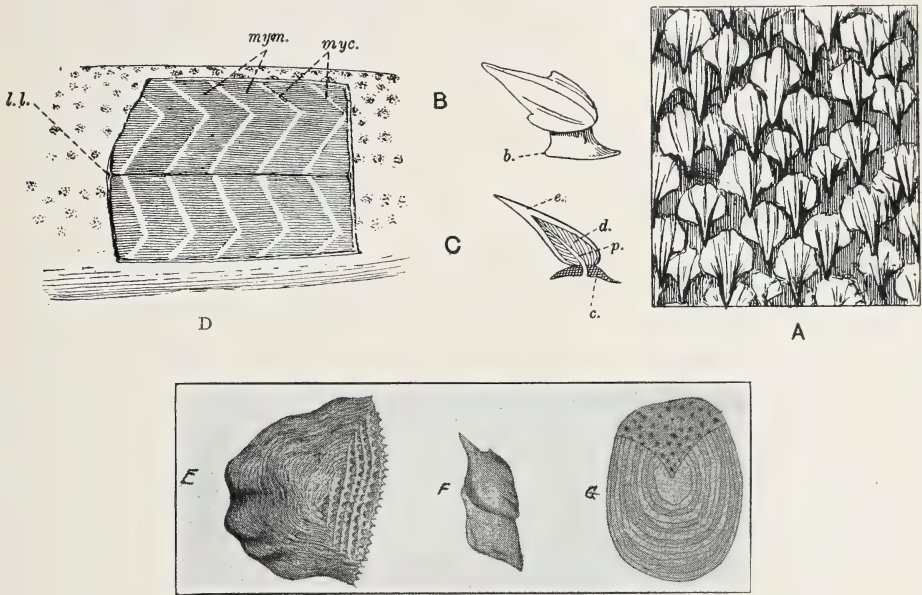


Fig. 401.

Pisoid scales. *A*, A portion of the skin of the dogfish as seen under a hand lens; *B*, a single scale removed from the skin; *C*, the same in section (diagrammatic). *b.*, Base of the scale; *c.*, the same in section; *d.*, dentine; *e.*, enamel; *p.*, pulp cavity. *D*, Part of the tail of a dogfish seen from the left side, with a piece of the skin removed. *l.l.*, Tube of the lateral line; *myc.*, mycommata or septa of connective tissue; *mym.*, myomeres. (After Borradaile.)  
*E*, ctenoid; *F*, ganoid; and *G*, cycloid scales. (From the Cambridge Natural History; *E*, *F*, after Günther; *G*, after Parker and Haswell.)

retained the original character, inasmuch as teeth often form on and in these bones.

In the higher forms, the dermal bones, however, arise from various centers of ossification in the cutaneous mesenchyme, and while this difference has been explained as a curtailing of the previous race history, it is quite likely that there is little difference between dermal and cartilaginous bone formation in the highest mammalian forms, the dermal being merely more "stretched out" portions, as will be learned when the endoskeleton is studied.

Scales in the teleosts, although often **rhomboid** when quite young, become circular later and are then called **cycloid**. **Ctenoid scales** are quite similar to **cycloid** except that they are set in **diagonal rows** in pockets of the dermis with their free edges overlapping. (Fig. 401.)

Amphibians do not have scales and hard exoskeletons, although there are extinct forms in which the body was covered with them.

In reptiles, the scales arise only from the epidermis and are, therefore, composed of horn or keratin. There is no trace of bone in them. The corium, however, furnishes the nourishment to these keratin scales, although it does not furnish any of the hard parts. There is no definite knowledge as to the relationship between the scales of reptiles and those of fishes.

Reptiles also have other integumental structures beside the keratin scales, namely: spines, combs, and claws; all, however, also made of keratin.

The birds are structurally and developmentally quite like the reptiles in that they possess feathers which are homologous to the reptile scales, and in having their beaks and claws composed of keratin. There have been toothed-birds in the past, and it is said that tooth-germs have even been found in the embryonic jaws of some of our modern birds.

In mammals, the tiny scales covering the body are seen as definite hard structures, mainly on the claws, tails, and sometimes on the backs of such animals as the armadillos (Fig. 387). They are always only epidermal in origin. In the armadillos, the corium secondarily supplies the hardening portions so that the covering of the animals becomes very thick, hard, and osseous.

It is assumed, very often, that formerly all mammals were covered by hard scales because the hair arrangement of mammals is quite like that of the scales. For example, on the tail of a rat, the scattered hairs will appear among the scales in a very definite relationship, namely, a group of three hairs (one medial and two lateral) will project beneath the margin of each. The median hair is the longer and stouter. In addition to this, there are similar arrangements of hairs in groups of three even upon areas not definitely associated with scales. The hairs, however, are arranged in an imbricated series like scales. Even where the hair is very thick, and forms a heavy fur, this arrangement can often be made out.

As scales in their simplest form are tiny elevations, the pads on mammalian feet are often used to illustrate the arrangement and transition of scales in different mammalian groups.

These pads are usually eleven in number, five for the tips of the digits, four for the distal margins of palm and sole beneath the interdigital intervals, and two for the wrist or ankle.

The scale rudiments are arranged in rows upon these pads. They fuse to form "friction ridges," so-called because they prevent the animal from slipping (Fig. 402). These friction ridges are always arranged at

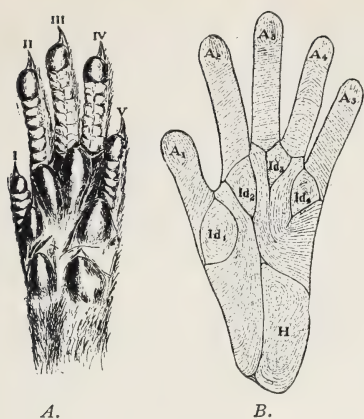


Fig. 402.

Ventral view of the palm of the hand of an insectivore and of a primate to show correspondence between relief and arrangement of friction ridges. *A*, *Crocodyura caerulea* (shrew-mouse). Forepaw showing walking-pads enclosed by triangular folds of skin. *B*, *Macacus sp?* (Old World monkey). Hand, covered by friction ridges, the arrangement of which corresponds to the relief of *A*. The pads are represented by concentric circles, and the triangular folds by triradii. These latter features are here designated by heavy lines, although in the animal they are no more conspicuous than the others. (From Wilder after Miss Whipple.)

to all truth wherever and whenever found. But our prejudices and wishes all too often influence us as readily toward a too conservative as toward a too radical point of view. We must face the facts as they are, pleasant or unpleasant, but we must not forget that **many different interpretations can be drawn from the self-same facts**. An example of this is brought home at this very point.

There is no question about the facts so far presented, which anyone can demonstrate for himself. The question that presents itself is simply this: Does it follow that because a bird has all the characteristics of a reptile, **plus some additional features**, that, therefore, it had reptile ancestors?

If one accept the so-called Haeckelian law of biogenesis, that each individual in the embryonic stage passes through the adult stages of the race to which it belongs, then such a conclusion is valid; but, if we remember that all this so-called law means is that all forms pass through **similar** stages, the higher forms then continuing, while the lower ones remain stationary, another interpretation is still more valid. And our difficulty is by no means lessened when we remember that biologists at large are agreed that acquired characteristics **are not transmitted**. What, then, becomes of even a reasonable explanation of how any modifications can be carried on from parent to offspring?

Still further, we have seen from Professor de Vries' work that all newly appearing structures may be but the return of some **recessive**

right angles to the direction in which there is considerable tendency to slip. In the arbooreal types of mammals, such as the lemurs and monkeys, the scale rudiments are arranged in concentric circles, as in such animals there is a tendency to slip in any and all directions. The ridges form only on the actual contact surfaces.

While structure always **determines function**, yet in integumental studies we have found that function very decidedly **modifies the various structures**, and later, we shall see that such modification is not confined to integument alone.

Now, to be truly scientific, means to retain an open mind

characters which have long lain dormant, while in the so-called **rudimentary structures** there is always the alternative of considering such structure an **overgrowth** or a **hypertrophy** of some smaller organ valuable at some time in embryonic life; or, it may even be a true remnant of a structure no longer needed by modern methods of life, modern foods and modern environment. Or, still a third alternative suggested by Professor Bateson, that just as a complex structure is **the more complex, the smaller and simpler it can be made to appear**, so the original fertilized egg-cell, from which an entire vertebrate develops, is much more complex than the finally completed body, because the single cell had all the possibilities of the complete body within its tiny self, and consequently, we are always really losing something as development proceeds.

What is meant by a **normal development** of a cell into what it is later to become, is simply, that commonly, certain obstacles are removed by which these possibilities can come forth. If then, either environment (external or internal), food, atmosphere, position, injury, or chemical stimulus removes certain factors which hold back growth, any such possible factor already present in the cell may come forth; but its possibility must have been already present in the primitive cell.

This is well shown by the fact that normally the skin finishes growth at a certain time, but if a portion of skin is torn, the injury stimulates the connective-tissue cells which then divide and fill the wound with scar-tissue, that is, the original injury **removes an obstacle** to such connective-tissue-cell's growth. What particular factors, then, can be said to explain modifications? We do not know.

It is the province of science to press a problem further and further back and thus raise more problems. There is, and can be, **nothing absolute about any scientific interpretation**.

The student, as does the average man, wants something definite, something he can be sure of; but this is just what he cannot find in any biological study; and, unless he can appreciate this and still love science—science is not for him.

If he should nevertheless go into a scientific field such as medicine or dentistry, he will be a practitioner who will ever seek and follow the opinions of the least scientific and least trustworthy men, simply because these speak with definiteness and absoluteness, albeit, likewise with absurdity.

## CHAPTER XXII

### THE ENDOSKELETON

**B**Y the term skeleton we mean all **hard parts** used for **support and protection** outside of what has already been termed the **integument**. The skeleton develops only from **mesenchyme**. It will be recalled that after the mesoderm has divided into a somatic and a splanchnic layer, these two layers together are called **mesothelium** to distinguish them from the mesenchyme. The latter, while also lying in the segmentation cavity, develops as **separate cells from both the mesothelium and the entoderm**. Some even believe that ectoderm has a part in its formation.

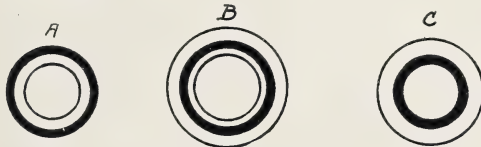


Fig. 403.

Diagram to show growth of bone. *A*, animal recently fed madder which causes a layer of bone (black) to be colored by the dye; *B*, no madder fed for a time, when a deposit of colorless bone on outside of colored layer is formed; *C*, later the outer layer becomes thickened and the inner layer is absorbed.

When bone forms from cartilage, the lime salts may be laid down on the inner portion of the **perichondrium** and from there invade the cartilage. This is called ossification by **ectochondrostosis**.

Bones may form from cartilage of the osteoblasts or, forming from the more interior cells and then, with this group of osteoblasts as an ossification center, ossification extends in all directions. This latter method is known as **entochondrostosis**.

Often the long bones increase by the formation of smaller bones which then become attached to the ends of the long bones. Such joining is called an **epiphysis**.

If madder is fed to an animal, the actual bone formation is colored. This makes it possible to see just how the new bone is formed. The new bone is laid down outside of that already grown, and with such growth the "marrow cavity" becomes larger by a resorption of the bone which has already formed. The osteoblasts are laid down in between the newly forming layers of bone (Fig. 403).

### THE VERTEBRAL COLUMN

We have already seen, in our study of the embryology of the frog and chick, how the centra of the vertebrae are formed around the notochord and that possibly some parts of the chorda remain as the intervertebral discs. Here we are to study and compare the adult form in the various groups.

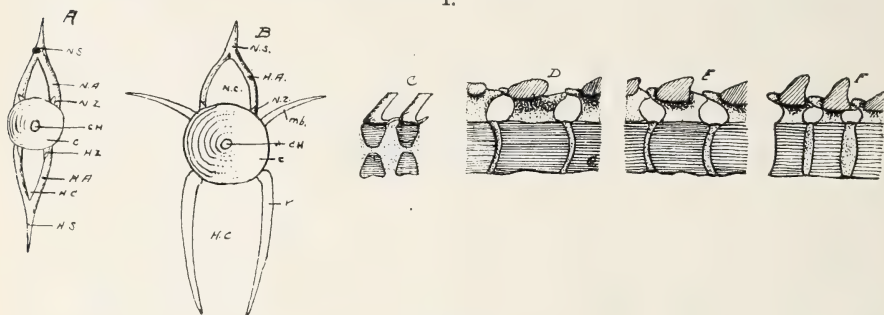
The most complete vertebrae may be found in the tails of some of the lower vertebrates. Figure 404 shows a comparison of several types.

It will be noticed that dorsally there is a neural **arch**, while ventrally a similar outgrowth from the centrum is known as the **haemal arch**, while the pointed end in each case is known as a **spine**.

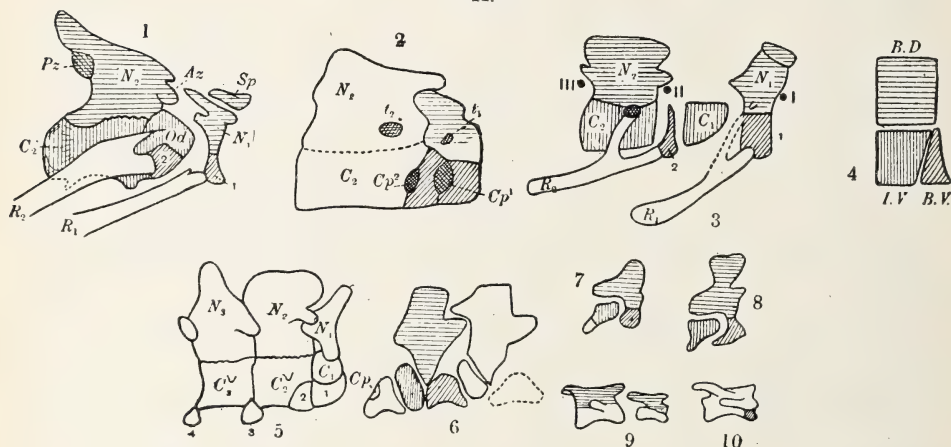
The haemal arch is quite incomplete or even entirely absent in the regions anterior to the tail.

In the higher vertebrates (Fig. 404) there are articular processes,

## I.



## II.



## III.

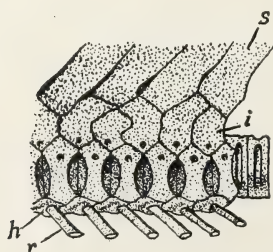


Fig. 404.

I, A and B. Diagram of a vertebra of a bony fish. A, caudal; B, trunk; C, amphicoelous; D, procoelous; E, opisthocelous; F, amphiplatyan vertebrae. The head is supposed to lie at the left. c, centrum or body of vertebra; ch, notochord; h.a., haemal arch; h.c., haemal canal; h.s., haemal spine; h.z., haemal zygapophysis

called **zygapophyses**, both on the anterior and posterior sides of each vertebra, and usually **transverse processes** extending laterally in the planes of the original divisions between the muscles.

Where true ribs occur, there are two additional transverse processes to which these attach.

The centrum, where it meets with the intervertebral disc, has four distinct forms (Fig. 404).

If the face of the centra at each end, where it is to meet with the intervertebral disc of the centra lying immediately anterior and immediately posterior to it (as in fishes), is **hollow** at both ends, it is called **amphicoelous** (Fig. 404). If one end is like a ball, namely, convex, and the other concave, so that the ball-like portion can fit into it, the condition is known as **procoelous** if the socket lies on its anterior surface, and **opisthocelous** if on the posterior surface, while if the ends of the centra are flat, as they usually are in mammals, such a condition is known as **amphiplatyan**.

The arches of the vertebrae form first (Fig. 352), and the centra later, and the sclerotome divides into a caudal and cranial half which thus makes possible an advantageous condition to the animal in permitting interaction of skeleton and muscles (Fig. 305).

It must be remembered, however, in this connection, that in some animals normally, and in others abnormally, the two halves of the sclerotome may unite (as in some fishes), and thus not have this interplay of muscles; or two neural arches may form by the rudiment which normally becomes one arch, dividing as does the sclerotome, and thus produce a greater quantity of vertebrae than usual. And, not only may this happen to the neural arches, but also to the centra. In fact, almost any variation in the spinal column may be accounted for by an embryological condition remaining in the adult form.

or articulating facet; *m.b.*, intermuscular bone; *n.a.*, neural arch; *n.c.*, neural canal; *n.s.*, neural spine; *n.z.*, neural zygapophysis; *r.*, rib.

II. Composition of vertebrae of Reptiles, illustrated by the first and second cervical vertebrae. (1) Atlas (first cervical) and axis (second) vertebrae of Crocodile. (2) Atlas and axis of *Metriorhynchus*, a Jurassic Crocodile. (3) Analysis of the first two cervical vertebrae of a Crocodile. 2, second basiventral complex or "intercentrum" continued upwards into the meniscus or intervertebral pad. (4) Diagram of the fundamental composition of a Reptilian vertebra or other amniotic, gastrocentrous vertebra. (5) The first three cervical vertebrae of *Sphenodon*. (6) Trunk-vertebrae of *Eryops*, a Permian Proreptile, typically *temnospondylous*. *cp*, articular facet of the capitulum of a rib. (7) The complete atlas of an adult *Trionyx hurum*. The second basiventral (intercentrum) is attached to the posterior end of the first centrum which, not being fused with the second centrum, is not yet an odontoid process. (8) The complete atlas of an adult *Trionyx gangeticus*, still typically *temnospondylous*. (9) The first and second cervical vertebrae of an adult *Platemys*. (10) The complete atlas of a *Chelys fimbriata*. *Az*, Anterior zygapophysis; *B.D*, basidorsal; *B.V*, basiventral; *C<sub>1</sub>*, *C<sub>2</sub>*, *C<sub>3</sub>*, first, second and third centra, formed by the intervertebra; *Cp<sup>1</sup>*, *Cp<sup>2</sup>*, articular facets of the capitular portions of the first and second ribs; *I*, *V*, Intervertebral; *N<sub>1</sub>*, *N<sub>2</sub>*, *N<sub>3</sub>*, first, second and third neural arch; formed by the basidorsalia (*B.D*); *Od*, odontoid process (which is the first centrum); *Pz*, posterior zygapophysis; *R<sub>1</sub>*, *R<sub>2</sub>*, ribs; *Sp*, detached spinous process of the first neural arch *t<sub>1</sub>*, *t<sub>2</sub>*, tubercular attachments of the first and second ribs; 1, 2, 3, 4, "intercentra" (which are the basiventrals); *I*, *II*, *III*, position of the exit of the first, second and third spinal nerves.

III. Trunk vertebrae of a tropical Skatē. *h*, haemal process; *i*, intercalary plate; *n*, neural process; *r*, rib; *s*, spinous process. (II, After Gadow: III, from Kingsley after Dumeril.)

As the ventral nerve root usually penetrates the caudal division of the halved sclerotome, and the dorsal root passes between the two divisions of each sclerotome but penetrates the cranial portion, one can tell in the adult, from following these nerve roots, which of the adult structures come from cranial and which from caudal halves.

The different shaped ends of the centra, which have already been mentioned, are brought about after the vertebrae are quite definitely formed. The centra with their arches are in a quite definite position and the centra cannot, therefore, grow any more except at the ends. These may have more substance laid down in the intervertebral regions, however, and thus ultimately come to be amphicoelous, procoelous, opisthocelous, or amphiplatyan.

### REGIONS OF THE VERTEBRAL COLUMN

The regions of the spinal column are:

- (1) **Cervical.** The neck region, either without ribs of any kind or the ribs are smaller than in the other regions.
- (2) **Thoracic.** These have distinct ribs attached.
- (3) **Lumbar.** Following the thoracic, and without ribs.
- (4) **Sacral.** This region includes one or more vertebrae with which the pelvic girdle is connected.
- (5) **Caudal.** The tail-portion immediately following the sacrum.

These divisions are quite distinct in the higher vertebrates, but in the lower, any and all combinations may form, so that the ribs may extend almost the entire length of the spinal column. In such cases all vertebrae having ribs are called **dorsal**.

In fishes, snakes, and whales, the sacral region cannot be distinguished; and in fishes, the dorsal and cervical vertebrae are quite indistinguishable. In this latter case there are, therefore, only trunk or abdominal vertebrae, and caudal vertebra, the line being drawn where the haemal arches begin to have ribs attached.

The first cervical vertebra to which the skull is articulated is called the **atlas** in all higher vertebrata, while the second cervical vertebra, at least in the amniotes, is called the **axis** or **epistropheus** (Fig. 404).

In mammals the atlas can always be distinguished by the two anterior articulating surfaces for the two condyles of the skull, and the axis, by the tooth-like projection known as the **odontoid process**, on which the atlas turns.

It is interesting to note that embryologically, this tooth-like process develops from the atlas, but then separates and later becomes attached to the next succeeding vertebra.

In a few reptiles there is a so-called **proatlas**, consisting of one or two plates lying between the atlas and the skull. It is not known just what relationship this bears to the other vertebrae.

In fin-bearing animals, if the spinal column runs to the end of the

body in a straight line (Fig. 405), the caudal fins are known as **diphycercal**, a condition found in the young of all fishes and in adult cyclostomes, dipnoans, and **crossopterygians**.

If, as in the elasmobranchs and ganoids, the tail axis bends abruptly upward at the end, but retains the dorsal fin-part and a portion of the ventral region, it forms what is called a **heterocercal tail**, while if there is the same upward bend of the spinal column but the ventral and dorsal fin-portions of the tail become alike as to size and shape, the tail is

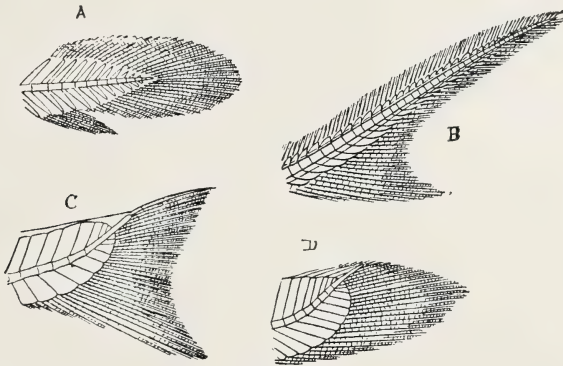


Fig. 405.

Diagrams of the principal forms of tails in fishes. *A*, protocercal fin (as in *Polypterus*); *B*, heterocercal (as in sharks); *C*, homocercal (as in most teleosts); *D*, homocercal (as in *Amia*). (After Folsom.)

said to be **homocercal**. Homocercal tails are brought about by the neural arches becoming smaller and the haemal arches becoming larger.

## THE SKULL

Bone either forms in cartilage or membrane, and it is quite common to hear biologists speak of cartilaginous and membranous bone. However, recent investigations lead us to believe that the so-called membrane is nothing more or less than cartilage drawn out very thin in those parts where the greatest pressure is produced. This can be understood the better if Fig. 406 be carefully studied. It will be noticed that all the superior and inferior boundaries are membranous, for here there is nothing to prevent a considerable extension of growth, while in the innermost portions, where pressure comes from practically all sides, it is cartilage.

Babies have a very soft spot on top of and close to the center of the head for about one and one-half years after birth. Places such as these are called **fontanelles**. These fontanelles are found during the embryonic period at **all spots** in the skull where several points of ossification come together. Ossification begins at many points, each center of ossification extending and growing toward each other. The fontanelle

is the unossified spot that constantly becomes smaller until ossification is complete.

Professor Eben J. Carey has recently shown that, contrary to the usually accepted idea that bone grows simply because there is an inner something which makes it assume definite forms, it is **the stress and pull and pressure of its location which determines its shape**, size, rapidity of growth, and even its joints.

The reason this has not been understood heretofore is that former experimenters took only sections from the growing bone itself for their study. Professor Carey, however, has taken the complete embryological structure, including all muscles and related portions, which might throw light upon the pull and pressure which affects such bone during its growing period.

Observing the ossification centers in the skull will throw light on this subject (Fig. 406). There are many such centers, and they are always found at exactly those points where there is an especial stress or pressure. At these points it may be that sharper bends in the blood vessels cause a slowing of the blood stream, which slowing in turn causes lime salts to be laid down at the angles to a much greater extent than where the blood stream can rush past more swiftly. Then, with each

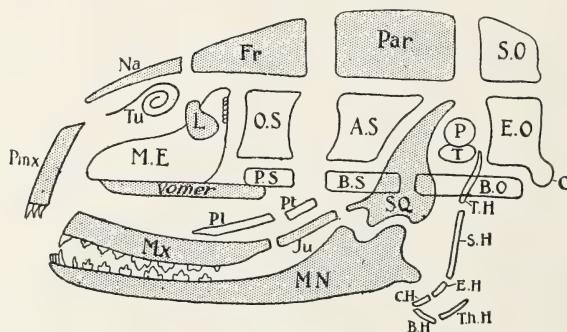


Fig. 406.

A diagram of the skull bones of a mammal, the membrane bones shaded. *B.O.*, Basioccipital; *E.O.*, exoccipital; *C*, condyle; *S.O.*, supraoccipital; *Par.*, parietal; *Fr.*, frontal; *Na*, nasal; *Pmx.*, premaxilla; *M.E.*, mesetmoid; *L.*, lacrimal; *Tu.*, turbinal; *P.S.*, presphenoid; *O.S.*, orbitosphenoid; *A.S.*, alisphenoid; *B.S.*, basisphenoid; *S.Q.*, squamosal; *P.*, periotic; *T.*, tympanic; *Pl.*, palatine; *Pt.*, pterygoid; *Mx.*, maxilla; *Ju.*, jugal; *T.H.*, tympanohyal; *S.H.*, stylohyal; *E.H.*, epihyal; *C.H.*, ceratohyal; *B.H.*, basihyal; *Th.H.*, thyrohyal; *vomer*; *MN.*, mandible. (From Borradaile, modified from Flower and Weber.)

succeeding deposit of such a hardening substance, a still greater number of blood capillaries is affected so that more lime is laid down, and so on, until all of the capillaries have been more or less obliterated and the entire cartilage, or membrane, has become ossified.

Beginning with the axial skeleton, the skull becomes our first object of attention. The **cranium** is that part of the skull which encloses the brain, together with those bony parts forming the eye-socket, the ear,

and the nose. The more caudal portion of the skull, which is directly connected with the cephalic end of the digestive tract, is called the **visceral skeleton**.

That portion of the skull which is cartilaginous is known as the **chondrocranium** while the membranous portion is called a **membrano-cranium**.

On each side of the notochord (which in the embryo extends as far forward as the infundibulum of the brain) a horizontal plate of cartilage is formed. These plates are known as **parachordal plates** (Figs. 310, 353). These extend laterally to the ears, forward to the end of the notochord, and backward to the exit of the tenth nerve. The **otic capsule** (cartilaginous) then grows about each internal ear and joins the parachordals. This forms a sort of trough in which the most caudal portion of the brain lies. The floor of this trough is known as the **basilar plate**, being formed of the parachordals and notochord as a floor, while the sense capsules constitute the sides.

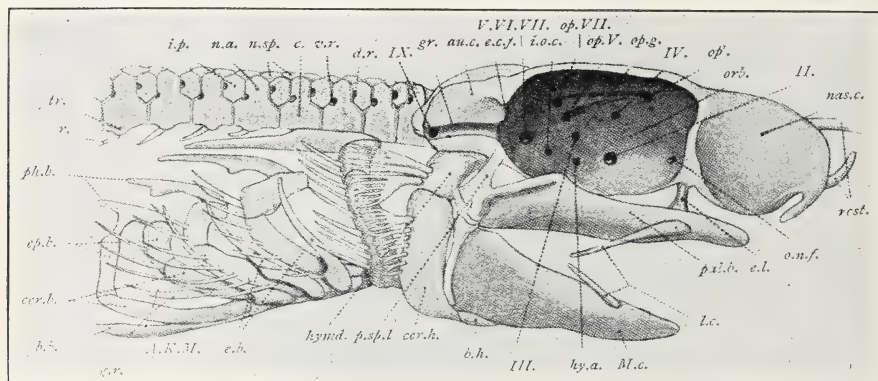
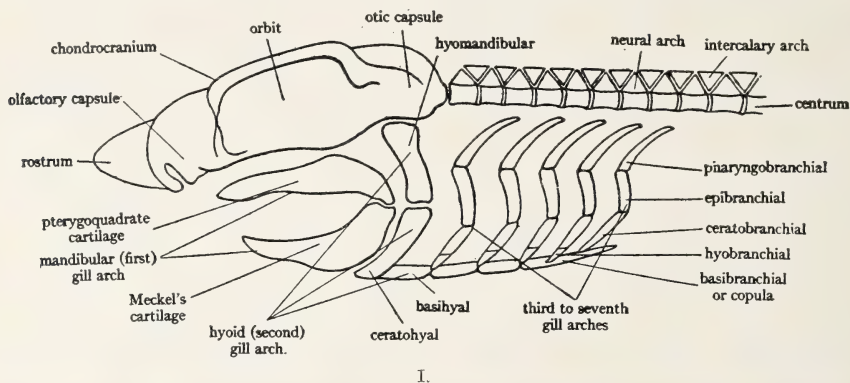
From this basilar plate two cartilages pass forward on each side, forming a similar trough for the anterior part of the brain. According to Professor Kingsley, the lower of these, called the **trabeculae cranii**, "join the anterior margin of the basal plate, while the **dorsal bars**, the **alae temporales** or **alisphenoid** cartilages, are eventually connected with the anterior wall of the otic capsules. In most vertebrates the trabeculae and alisphenoids develop as a continuum, but in some elasmobranchs they are at first distinct. The two trabeculae unite in front to form a **median ethmoid plate** beneath the olfactory lobes of the brain, beyond which they diverge as two horns, the **cornua trabeculae**, ventral to the nasal organs. The floor of the trough in front of the ears is formed by the ethmoid plate anteriorly, while behind, it is usually of membrane. In the elasmobranchs, cartilage gradually extends from one trabecula to the other, closing last below the infundibulum and hypophysis, these lying for a time in an opening (**fenestra**, later **fossa hypophyseos**), and after the closure, in a pocket in the floor of the chondrocranium, one of the cranial landmarks, the **sella turcica**."

"In the more primitive vertebrates, the trough is converted into a tube around the brain by the extension of cartilages between the alisphenoid cartilages and the otic capsules of the two sides dorsal to the brain. This roof, or **tegmen cranii**, is usually incomplete, having one or more gaps or **fontanelles**, closed only by membrane. In the higher vertebrates the cartilage roof is at most restricted to a mere arch, the **synotic tectum**, between the otic capsules of the two sides.

"Later a pair of nasal capsules develop around the olfactory organs. These are usually fenestrated and become united to the cornua, alisphenoids, and ethmoid plate. In a similar way a **sclera** (sclerotic coat) forms around each eye, but since the eye must move, this sense capsule never unites with the rest of the cranium. Behind the otic capsules

a varying number of (four in some sharks and most teleosts; in others three; in amphibia two), **occipital vertebrae** are developed, which later fuse with the rest of the chondrocranium. They alternate with myotomes and nerves in this region as do the vertebrae of the vertebral column.

"The cartilaginous **visceral skeleton** arises in the pharyngeal region which is weakened by the presence of the gill clefts. It consists of a series of pairs of bars, the **visceral arches** lying in the septa between the



II.

Fig. 407.

I. Diagram of the chondrocranium, vertebral column, and gill arches of an elasmobranch to show particularly the parts and relations of the seven gill arches. (Hyman's modification of Vialleton.)

II. Skull and part of the backbone of a dogfish, seen from the right side. The skeleton of the visceral arches has been pulled a little downwards. *au.c.*, Auditory capsule; *b.b.*, basibranchial cartilage; *b.h.*, basihyal cartilage; *c.*, centrum; *cer.h.*, ceratohyal cartilage; *cer.b.*, ceratobranchial cartilages; *d.r.*, *v.r.*, foramina for the dorsal and ventral roots of a spinal nerve; *e.m.*, extrabranchial cartilages; *e.c.f.*, external carotid foramen; *ep.b.*, epibranchial cartilages; *e.l.*, ethmoidal ligament; *gr.*, groove for vein which connects orbital and anterior cardinal sinuses; *g.r.*, gill rays; *hy.a.*, foramen for hyoidean artery; *hynd.*, hyomandibular cartilage; *i.o.c.*, interorbital canal; *i.p.*, intercalary plate; *M.c.*, Meckel's cartilage; *l.c.*, labial cartilages; *nas.c.*, nasal capsule; *n.a.*, neural arch; *n.sp.*, neural spine; *o.n.f.*, orbitonasal foramen; *op.V.*, *op.VII.*, foramina for ophthalmic branches of fifth and seventh nerves; *op'*, foramen through which combined ophthalmic nerves pass from the orbit to the snout; *op.g.*, grooves for *op.V.*, *VII.*; *orb.*, orbit; *p.s.p.l.*, postspiracular ligament; *pal.b.*, palatine bar; *ph.b.*, pharyngobranchial cartilages; *r.*, rib; *rost.*, rostrum; *tr.*, ventrolateral (so-called transverse) process. (After Borradaile.)

clefts, the bars of a pair being connected below the pharynx. Each bar, at first, is a continuous structure, but to allow for changes of size in the pharynx, each becomes divided into separate parts, while the arches become connected in the mid-ventral line by unpaired elements, the **copulae** (Fig. 407). The two anterior arches are specialized and have received special names, the first being the **mandibular**, the second the **hyoid arch**, the others, in the region of the functional gills, being called collectively **gill**, or **branchial arches**. The number of these last varies

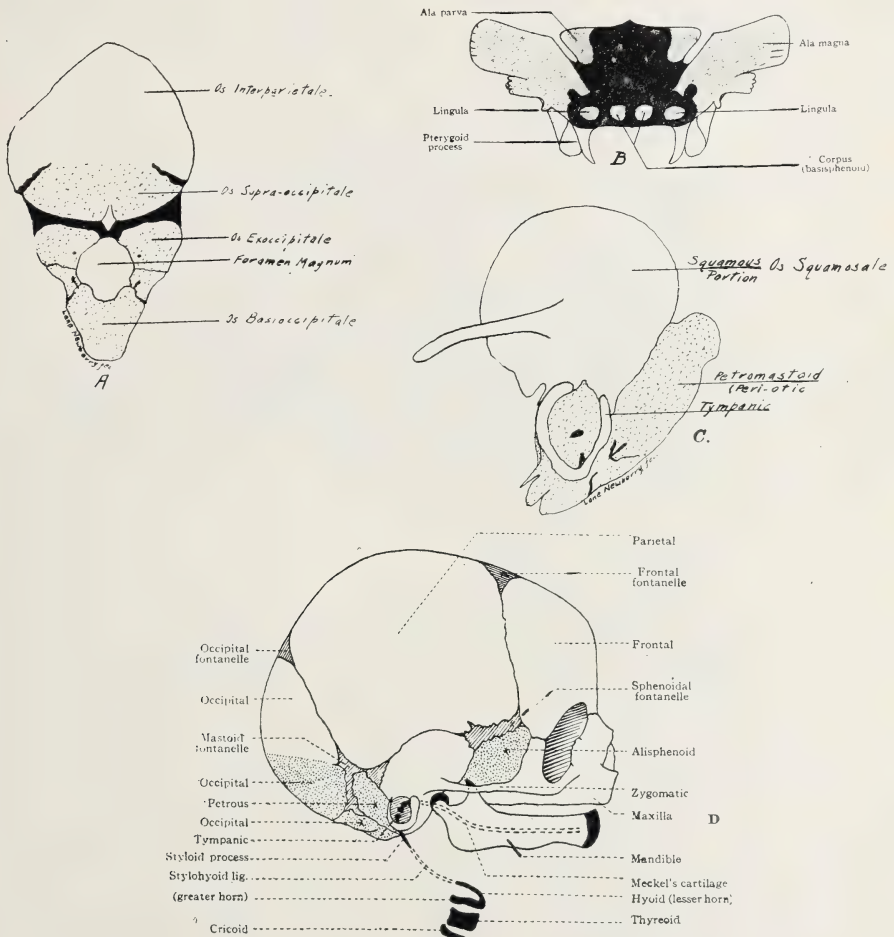


Fig. 408.

*A, B, C, Bones of early human skull to show their compound nature. A, occipital bone at birth showing the five elements of which it is composed. B, sphenoid bone in an embryo of four months. C, temporal bone at birth, showing its three components. Cartilage represented in black. (Redrawn from Sappey and Hyman.)*

*D, Diagram of skull of new born child. White areas represent bones of intramembranous origin; dotted areas represent bones (not derived from branchial arches) of intracartilaginous origin; black areas represent derivatives of branchial arches. (Combined from McMurrich and Kollmann.)*



in the higher fishes the hyomandibular becomes more separated from the ventral portion and tends to intervene between the mandibular arch and the cranium, becoming a **suspensor** of the jaws. Still higher it loses its suspensorial functions, becomes greatly reduced, and apparently is

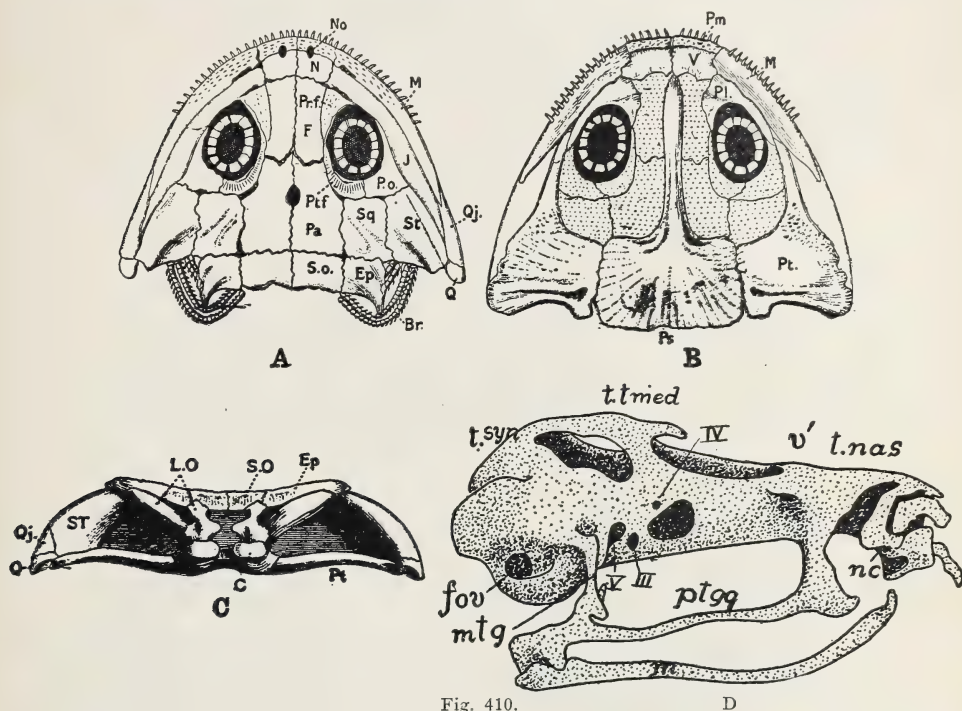


Fig. 410.

D

A, Dorsal and B, Ventral views of cranium of *Branchiosaurus salamandroides*, C, Posterior view of cranium of *Trematosaurus*. Br, branchial arches; C, condyle; Ep, epitotic; F, frontal; J, jugal; L.O., lateral occipital; M, maxillary; N, nasal; No, nostril; Pa, parietal; Pl, palatine; Pm, premaxillary; Po, postorbital; Prf, prefrontal; Pa, parasphenoid; Pt, pterygoid; Ptf, postfrontal; Q, quadrate; Qj, quadrato-jugal; S.o., supraoccipital; Sq, squamosal; St, Supratemporal; V, vomer. (After Gadow.)

D, Chondrocranium of a frog shortly after metamorphosis. fov, fenestra vestibuli; m, Meckel's cartilage; mtg, metapterygoid; nc, nasal capsule; ptgq, pterygoquadrate; tnas, tectum nasalis; tsyn, tectum synoticum; tmed, taenia tecti medialis; III-V, nerve exits. (From Kingsley after Gaupp.)

subsidiary to the sense of hearing or it may be lost, the question not being decided. The hyoid proper becomes more or less intimately connected with the arches behind and also is largely concerned in affording a support for the tongue.

"The branchial arches are all similar to each other in the lower vertebrates, but with the loss of branchial respiration in the higher groups, they tend to become reduced, the reduction beginning behind. Some may entirely disappear, others give rise to the laryngeal cartilages and the first may fuse with the hyoid. The first arch is in the region of the ninth nerve; the others in that supplied by the tenth."

Here<sup>1</sup> it will be necessary to review the frog skull very thoroughly, bearing in mind that, as in all vertebrates, the **occipitals**, the **two sets of**

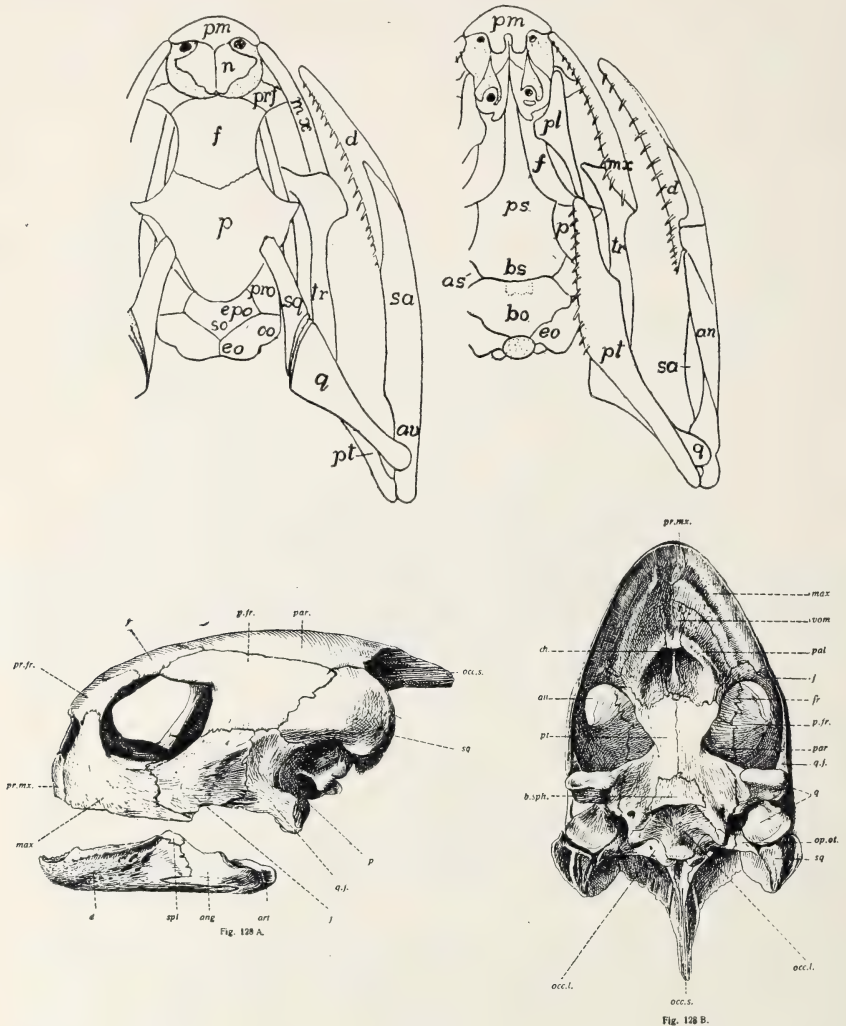


Fig. 411.

Upper two views, skull of snake. *an*, angular; *av*, articular; *bo*, basioccipital; *bs*, basisphenoid; *d*, dentary; *eo*, exoccipital; *epo*, epiotic; *f*, frontal; *mx*, maxillary; *n*, nasal; *oo*, opisthotic; *p*, parietal; *pl*, palatine; *pm*, premaxillary; *pro*, prootic; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *sa*, surangular; *so*, supraoccipital; *sq*, squamosal; *tr*, transversum. (From Kingsley after W. K. Parker.)

Lower two views, skull of turtle. *A*, lateral view. *B*, from below. *ang*, angular; *art*, articular; *au*, orbit; *b.sph.*, basisphenoid; *ch*, choanae; *d*, dentary; *fr*, frontal; *j*, jugular; *max*, maxillae; *occ.b*, basi-occipital; *occ.l*, lateral occipital; *occ.s.*, superior occipital; *op.ot.*, opisthotic; *pal*, palatine; *par*, parietal; *p.fr.*, postfrontal; *pr.mx.*, premaxillae; *pr.fr.*, prefrontal; *pt*, pterygoid; *q*, quadrate; *q.j.*, quadratojugal; *sq*, squamosal; *vom*, vomer. (After Schimkewitsch.)

<sup>1</sup>The frog does not have all the bones mentioned. All head bones that any vertebrate possesses are given in the list, so that the student must not expect to find any animal with all these structures, though he will find no vertebrate with head-bones not mentioned here.

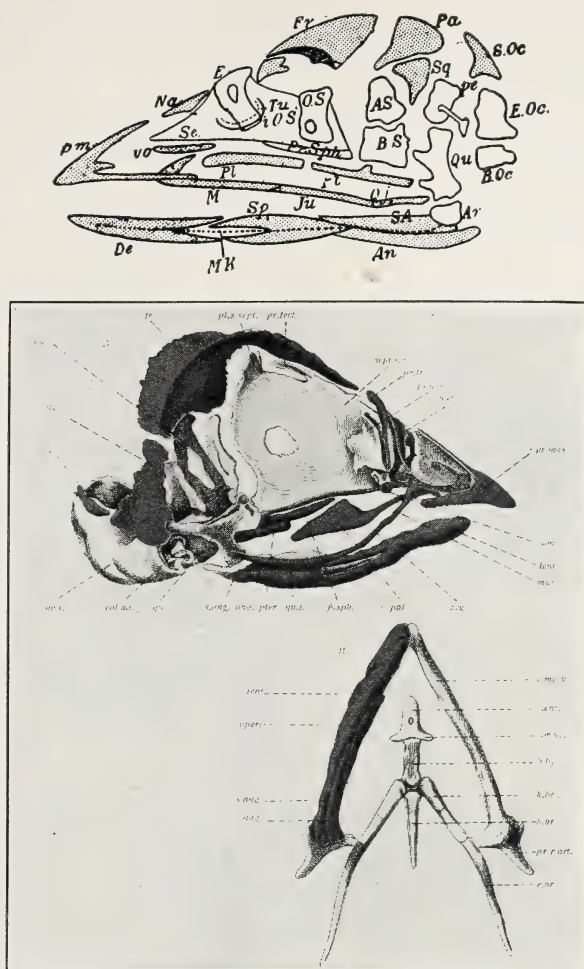


Fig. 412.

Upper view, a diagram of a bird's skull, disarticulated. (After Gadow.) Membrane bones shaded. *B.Oc.*, basioccipital; *E.Oc.*, exoccipital; *S.Oc.*, supraoccipital; *Pa.*, parietal; *Fr.*, frontal; *Na.*, nasal; *pm.*, premaxilla; *M.*, maxilla; *Ju.*, jugal; *Qu.*, quadrato-jugal; *Qu.*, quadrato; *Pl.*, palatine; *Pt.*, pterygoid; *pe.*, periotic; *Sq.*, squamosal; *AS.*, alisphenoid; *B.S.*, basisphenoid; *O.S.*, orbitosphenoid; *Pr.Sph.*, presphenoid; *vo.*, vomer; *i.Os.*, interorbital septum; *E.*, ethmoid; *Sc.*, nasal septum; *De.*, dentary; *Sp.*, splenial; *An.*, angular; *SA.*, supra-angular; *Ar.*, articular; *MK.*, Meckel's cartilage.

Lower views, model of developing chick-skull. *A.*, profile view, and *B.*, hyoid apparatus, as seen from below. *ang.*, Angular; *b.br.*, basibranchial; *b.hy.*, basihyal; *c.aud.*, auditory (otic) capsule; *c.ent.*, entoglossal cartilage; *c.meck.*, Meckel's cartilage; *col.au.*, auditory columella; *cor.hy.*, cornua of the hyoid; *dent.*, dentary; *e.br.*, epibranchial; *fr.*, frontal; *k.br.*, ceratobranchial; *l.*, lacrimal; *max.*, maxillary; *nas.*, nasal; *operc.*, opercular; *pa.*, parietal; *pal.*, palatine; *pl.a.o.*, anteorbital plane; *pl.s.sept.*, supraseptal plane; *pl.sph.l.*, sphenolateral plane; *pr.fr.*, prefrontal; *pr.r.art.*, retroarticular process; *pr.tect.*, Processus tectalis (roof-forming); *p.sph.*, parasphenoid; *pter.*, pterygoid; *qu.*, quadrato; *qu.j.*, quadrato-jugal; *s.ang.*, supraangular; *sept.i.o.*, interorbital septum; *sq.*, squamosal; *vom.*, vomer; *zyg.*, zygomatic process. (After Gaupp.)

sphenoids, and the ethmoids are the four groups constituting the cartilaginous cranium. (Compare Figs. 407, 409, 410, 411, 412, 413, 414.)

The occipital is divided into:

A supraoccipital, an exoccipital, on each side, and a basioccipital. These four bones form the borders of the foramen magnum.

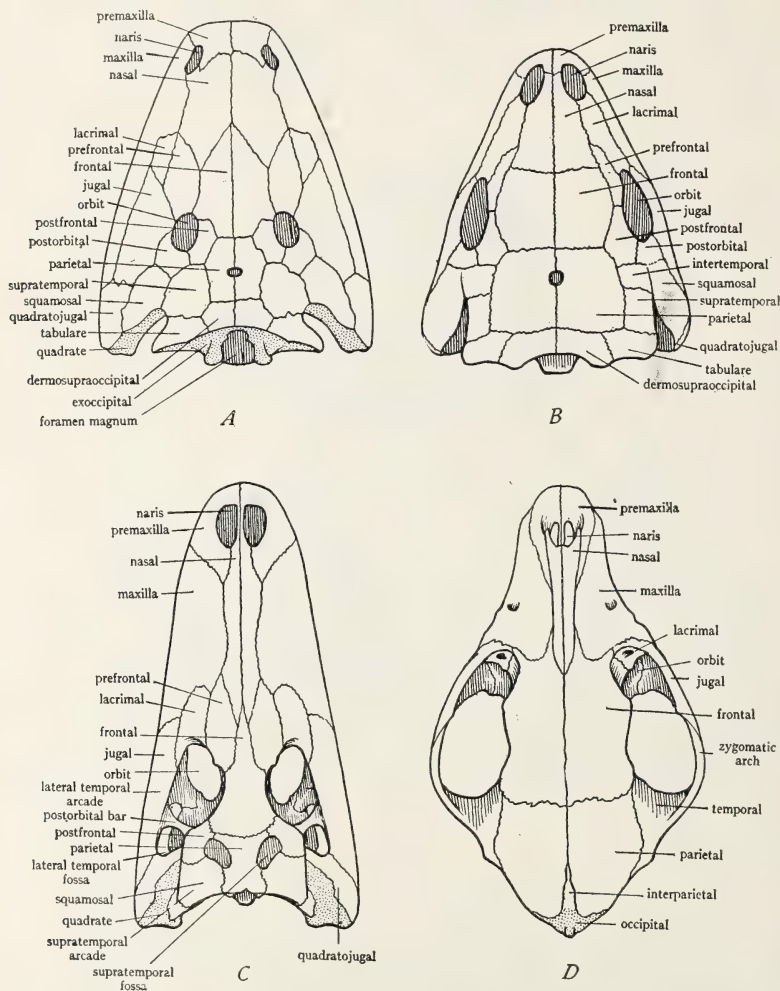


Fig. 413.

Dorsal view of the skulls of four representative vertebrates to show changes and reduction of the membrane bones of the roof. *A*, skull of an extinct amphibian, *Capitosaurus*, belonging to the *Stegocephala*; note the large number of membrane bones completely roofing the skull. *B*, skull of one of the most ancient reptiles, *Seymouria*, belonging to the *Cotylosauria*; the membrane bones are nearly as numerous as in the amphibian, are similarly arranged, and completely roof the skull. *C*, skull of a modern reptile, the alligator; several of the membrane bones which were present in the extinct forms have been lost, and the roof has several openings. *D*, skull of a modern mammal, the dog, showing still greater loss of membrane bones. Membrane bones blank; cartilage bones stippled. (From Hyman's "A Laboratory Manual for Comparative Vertebrate Anatomy," *A*, after Reynolds, *B*, after Williston, by permission of the Chicago University Press.)

The **sphenoids** are:

The **basisphenoid**, extending forward to the sella turcica.

The **presphenoid**, extending from the trabeculae to the ethmoid plate.

The **alisphenoid**, closely related to the basisphenoid.

The **orbitosphenoid**, in close relation with the presphenoid.

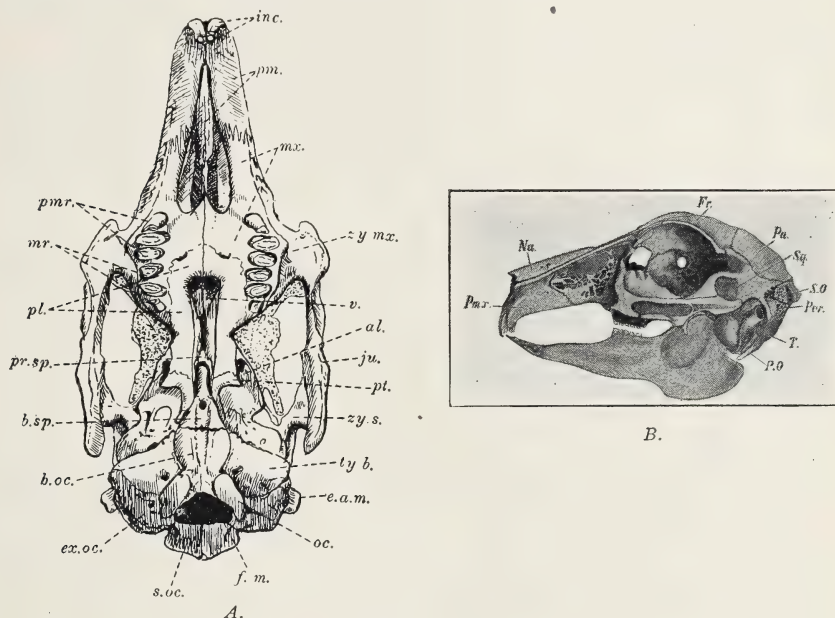


Fig. 414.

*A*, A ventral view of the skull of a rabbit: *al*, External process of the alisphenoid; *b.oc.*, basioccipital; *b.sp.*, basisphenoid; *e.a.m.*, external auditory meatus; *ex.oc.*, exoccipital; *f.m.*, foramen magnum; *inc.*, incisors; *ju*, jugal; *mr.*, molars; *mx.*, maxilla; *oc.*, occipital condyle; *pl.*, palatine; *pm.*, premaxilla; *pmr.*, premolars; *pr.sp.*, presphenoid; *pt.*, pterygoid; *s.oc.*, supraoccipital; *ty.b.*, tympanic bulla; *v.*, vomer; *zy.mx.*, zygomatic process of maxilla; *zy.s.*, zygomatic process of squamosal. (From Borradaile.)

*B*, A side view of a rabbit's skull. *Pmx.*, premaxilla; *Na.*, nasal; *Fr.*, frontal; *Pa.*, parietal; *Sq.*, squamosal; *S.O.*, supraoccipital; *Per.*, periotic; *T.*, tympanic (the reference line points to the bony external auditory meatus, beneath it lies the inflated bulla); *P.O.*, paroccipital process. (From Thomson.)

The **ethmoids** are divided as follows:

**Mesethmoid**, lying medially.

**Ectethmoid**, one on each side of the mesethmoid.

The **ectethmoid** becomes the ectethmoid labyrinth which comes to lie between ectethmoid and mesethmoid. The **turbinate** bones are sometimes added here.

From the **otic capsule** are developed various otic, or **petrosal**, bones.

These are usually divided into:

**Prootic**, lying in front of the ear.

**Opisthotic**, lying behind, although usually meeting below with an

**Epiotic** and a **sphenotic**, in the teleosts and a few other forms developed from the lateral wall of the otic capsule and lying in front and the

**Pterotic**, lying behind and directly above the horizontal semicircular canal of the ear.

The otic bones usually fuse and form a **petrosal bone** in all the higher forms. This lies directly between the lateral parts of the basi-occipital and the sphenoid.

A **ring of sclerotic bones** is often formed from the sclera of the eye of birds and reptiles, though these never unite with the regular bones. From the nasal capsules a **lateral ethmoid** often forms on the upper wall, while the **turbinate bones** form on the medial and lateral walls. In man the single occipital bone is formed by the four occipitals mentioned above. The single sphenoid is a fusion of the six sphenoids mentioned above, the **alisphenoids** form the greater wings and the **orbito sphenoids** the lesser ones. (Fig. 408.) The ethmoid is similarly made up of the various ethmoids mentioned.

The **membranocranium** gives rise to the following bones:

**Nasal**, covering the olfactory region.

**Frontals**, between the orbits.

**Parietals**, on the same level with the otic capsules.

**Inter-parietal**, unpaired, between parietal and supraoccipital.

While these are practically all of the membranocranial bones in the roof of the cranium of the higher forms, others may appear in the lower groups. For example:

**Supratemporal**, lying lateral to each parietal.

**Postfrontal**, behind the orbit.

**Postorbital**, forming the posterior wall of the orbit.

**Supraorbital**, taking the place of the frontal in forming the superior or medial wall of the orbit.

**Prefrontal**, bounding the orbit in front.

**Lacrimal**, lying lateral to the prefrontal.

**Intertemporal**, lying dorsal or medial to the alisphenoid.

**Postparietal**, between parietals and interparietals.

**Epiotic**, lying above each otic capsule and usually called the **tabulare**.

If, as in some fish, birds, and reptiles, the basilar plate and trabeculae fail to ossify, then the roof of the mouth, which is, of course, the frontal of the cranium, is also a membrane bone called the **parasphenoid**, while farther forward the **vomers** or **plough-share bones** are also membranous and lie in the nasal region. Both parasphenoid and vomers may bear teeth.

As soon as bone begins to form, the **pterygoquadrate** changes considerably, becoming closely connected with the cranium in front. The middle portion disappears and the **palatines**, a pair of membrane

bones, replace the disappearing part. The remaining portion of the visceral arch ossifies, usually though not always, forming two bones on each side, the paired **anterior pterygoid** and the paired **posterior quadrate**. These now become the **suspensor** of the lower jaw. In some forms such as the teleosts and the reptiles, there appears an entire series of pterygoid bones.

Outside of the pterygoquadrate, a second arch of membrane bone develops to form the functional upper-jaw in all bony vertebrates. This when fully developed consists of:

**Squamosal**, underlying the quadrate.

**Quadratojugal**, which follows immediately.

**Zygomatic**, also called the **malar** or **jugal**.

**Maxillary**.

**Premaxillary**, which forms the tip of the jaw.

Only the maxillary and premaxillary bear teeth.

When, as in the higher forms, such as man, the roof of the skull is not continuous, but openings of various kinds are seen, such openings are known as **fossae**. The more common and constant are as follows:

**Infratemporal**, being the most lateral.

**Supratemporal**, which is separated from the foregoing by the **squamoso-postorbital bars**.

**Posttemporal**, lying between the parietal, supratemporal, and occipital bones.

**Temporal**, when infra and supra temporal fossae unite.

Any of the bones mentioned above may fuse or disappear entirely in certain groups, while in others there may be connections quite different from the usual type.

The lower jaw is by no means modified as extensively as the upper. **Meckel's cartilage**, by an ossification, gives rise to two bones in each half of the lower jaw. There is an **articular bone (articulare)** where the jaw meets with the quadrate, and at the tip where both sides unite—the **symphysis**—there may be a **mento-Meckelian** bone, although this does not occur often. The rest of Meckel's cartilage forms an axis about which the membrane bones of the lower jaw are arranged. These are as follows:

(1) **Dentary**, surrounding the Meckelian in front and bearing teeth.

(2) **Splénial**, on the inner side behind the dentary and often bearing teeth.

(3) **Angulare**, on the lower side usually extending back to the hinder end of the jaw.

(4) **Surangulare**, lying on the outer posterior part of the jaw.

(5) **Coronoid**, on the upper side of which muscles which close the jaws, are attached.

(6) **Goniale**, also called **antarticular** or **dermarticulare**, lies on the medial and ventral sides of the articulare with which it usually fuses.

The dentary, splenial, and angulare are usually found, but very few vertebrates have them all.

In the hyoid and branchial arches, the outside portions are known by the same names as the corresponding cartilages, membrane bones never being found here.

The method by which the jaws are suspended varies. If the pterygoquadrate is directly connected with the cranium, as in a few elasmobranchs, the suspension is called **amphistylic**. If it is held in place by ligaments and the hyomandibular is interposed between the otic capsule and the hinder end of the jaw, it is called **hyostylic**; while, if the pterygoquadrate is more or less fused with the cranium, as in all the higher forms beyond the fishes, it is known as **autostylic**.

### THE APPENDICULAR SKELETON

There are two types of appendages, namely: **median**, or **azygos**, which are found in aquatic vertebrates, and the regular **paired** appendages found in all other classes except the cyclostomes. Several theories have been advanced to account for the two types. One of these is that the two types of appendages have no relation to each other, and developed independently, the pelvic and pectoral girdles being supposed to have originated from the gill arches, while the appendage bones have been derived from that portion which normally supports the gills. The other view assumes that two longitudinal folds ran the full length of the body behind the head (Fig. 415), each of these folds being sup-

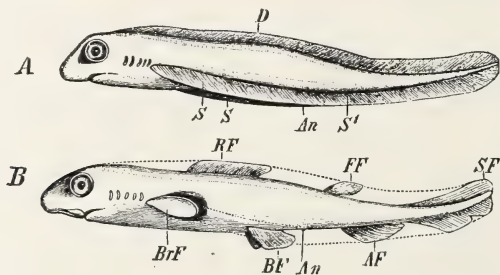


Fig. 415.

Diagrams showing *A*, the undifferentiated condition of the paired and unpaired fins in the embryo, and *B*, the manner in which the permanent fins are formed from the continuous folds. *AF*, anal fin; *An*, anus; *BF*, pelvic fin; *BrF*, pectoral fin; *D*, dorsal fin-fold; *DF*, dorsal fin; *S*, lateral folds which unite at *S'* to form ventral fold. (From Wiedersheim.)

ported by a series of skeletal rods. The two dorsal and two ventral folds then fused to form the dorsal and ventral fin. The anal opening is, however, on the ventral side. Consequently, the caudal fins had to be formed from the ventral fusion **behind** the anal opening, while the portion anterior to the anal opening develops into the appendages proper.

Both theories are unsatisfactory, the latter because there is no double origin of the dorsal fins, and the former, known as the **gill-arch-theory**, is unsatisfactory due to the fact that the paired appendages develop **outside the body musculature**, while the visceral arches are always internal.

All median appendages have the form of fins, and are termed **dorsal**, **terminal** (caudal), or **ventral** (anal). They may occur as a continuous fin, or they may be broken up with intervals between. Fins occur in all fishes, in the larval and tailed amphibians, and even in rather isolated groups, such as the **Ichthyosaurs** and the whales, although in the amphibians and the higher groups, there is no skeleton in the median fins.

The skeleton of the fins usually consists of definite metameric cartilaginous or osseous bars, each of which is divided into a proximal **basale** and a distal **radiale**. The basale often articulates or alternates with the spinous processes of the vertebrae. The radiale supports the fins proper.

In the higher forms of vertebrates, when the skeleton of the fins is not composed of cartilage or bone, there is a horny substance known as **elastoidin** which forms a number of slender rods in greater number than the somites. They arise from the corium just below the epidermis, often being united in bundles, and thus form soft-finned rays, often replacing the radiale.

### PAIRED APPENDAGES

An extinct shark had a pair of fins approximately in the region where pectoral and pelvic girdles normally form, but no satisfactory theory has yet developed as to how arms and legs were derived from this type of fin.

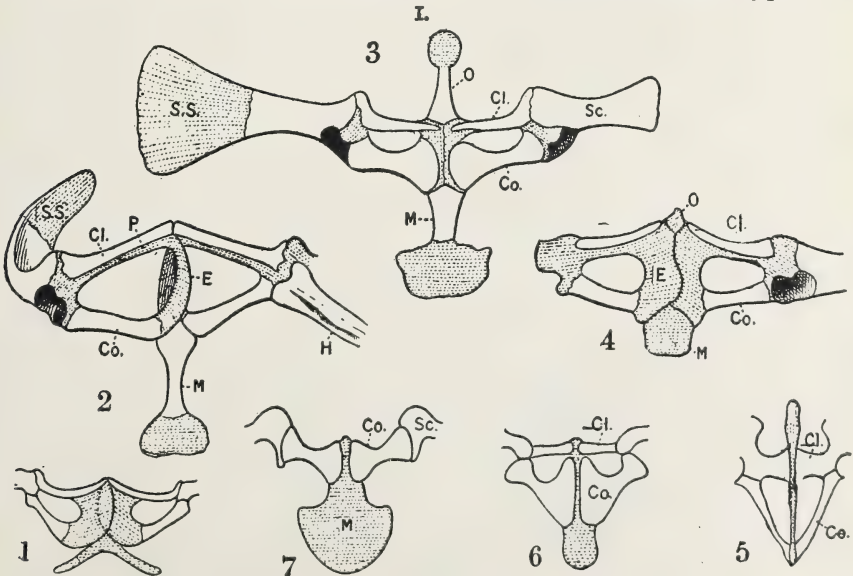
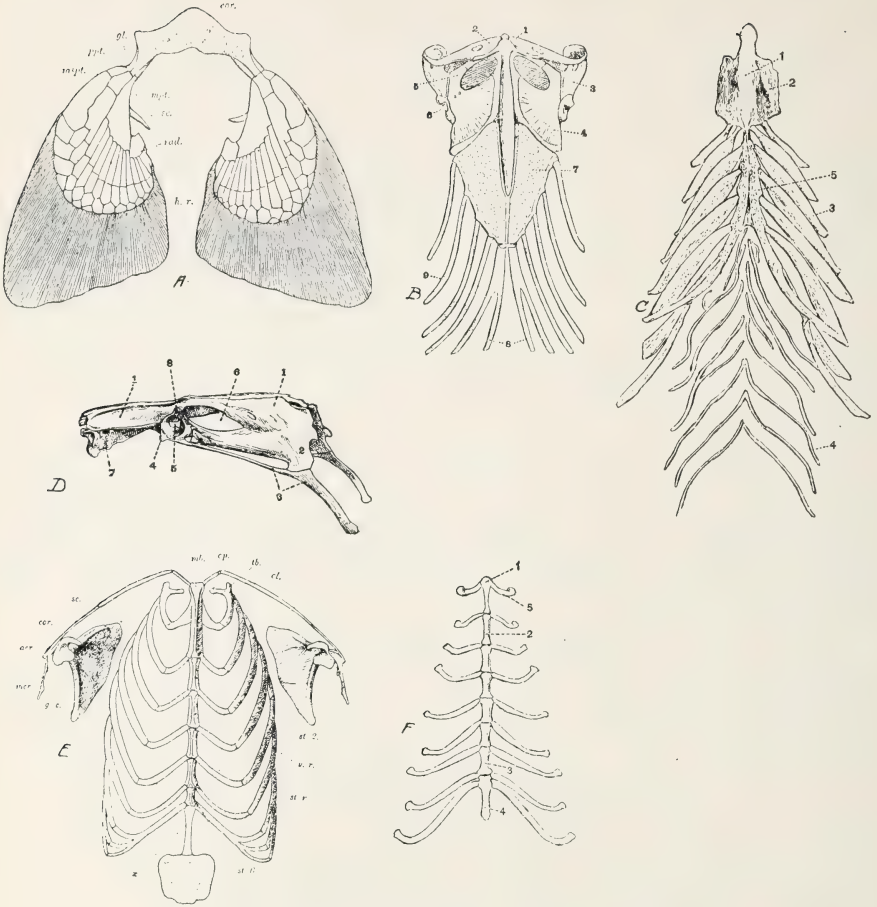


Fig. 416.

II.



III.

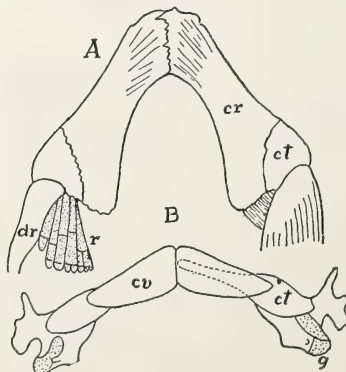


Fig. 416.

Shoulder girdles. I. Ventral views of the shoulder girdles of various Anura. (Slightly enlarged.) 1, *Bombinator igneus* (a species of Frog), and 2, *Bufo vul-*

The internal support of both shoulder and pelvic girdle consists of inverted arches across the ventral side of the body, the limbs of the arch extending dorsally. The part to which the limbs are attached is called the girdle. The arch itself always forms in cartilage, though membrane bone or dermal bone may be added.

The typical girdle consists of three elementary parts, one dorsal and two ventral, all of which meet at the point of attachment of the limbs, and all contribute to form the socket, in the forelimb called the **glenoid** and in the hindlimb known as the **acetabulum**. This shows why we consider pectoral and pelvic girdles and appendages homologues.

### THE SHOULDER GIRDLE (Fig. 416)

In fishes, the shoulder girdle is more or less U-shaped, with the glenoid fossa at the dorsal end. Immediately dorsal to the fossa lies the scapular region. Quite often, the dorsal part of the scapular region is again divided, so that a supra-scapula is formed. In the skates, the supra-scapula articulates with the adjacent vertebrae; usually, however, the entire girdle lies free from the axial skeleton. A pair of clavicles form from the skin. These overlay the **coracoid** region of the girdle, and meet in the midline, while a **cleithrum**, a second bone above the glenoid fossa, forms. In some of the ganoids, it is the cleithrum which extends toward the midline so as to take the strain; in fact, it is assumed that in higher groups, where the two halves of the cartilaginous girdle have separated, the separation is due to the stress laid upon these parts.

In the higher ganoids and in the teleosts, the cleithrum increases in

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*garris* (Toad) as examples of the arciferous type. 3, Adult, and 4, metamorphosing Frog, *Rana temporaria* showing change from the arciferous into the firmisternal type. 5, *Hemisus guttatus* (narrow-mouthed toad). 6, *Breviceps gibbosus* (tailless amphibia). 7, *Cacopus systoma* (narrow-mouthed toad). Cartilaginous parts are dotted. Ossified parts are white. *Cl.*, clavicle; *Co.*, coracoid; *E.*, epicoracoid cartilage; *H.*, humerus; *M.*, metasternum; *O.*, omosternum; *P.*, precoracoid; *Sc.*, scapula; *S.S.*, suprascapula. (From Gadow and Boulenger.)

II. *A.*, The skeleton of the pectoral fins and girdle of a dogfish, seen from the ventral side. (After Borradaile.) *cor.*, Coracoid region; *gl.*, glenoid surface; *h.r.*, horny rays; *mpt.*, metapterygium; *mspt.*, mesopterygium; *ppt.*, propterygium; *rad.*, cartilaginous rays; *sc.*, scapula. *B.*, Ventral view of the shoulder-girdle and sternum of a Lizard, *Loemantus longipes*. (After Parker.) 1. Interclavicle. 2. Clavicle. 3. Scapula. 4. Coracoid. 5. Precoracoid process. 6. Glenoid cavity. 7. Sternum. 8. Sternal bands not united. 9. Sternal rib. *C.*, Sternum and associated membrane bones of a Crocodile, *C. palustris*. (After Shipley and MacBride.) The last pair of abdominal ribs which are united with the epipubes by a plate of cartilage have been omitted. 1. Interclavicle. 2. Sternum. 3. Sternal rib. 4. Abdominal splint rib. 5. Sternal band. *D.*, Lateral view of the pelvis and sacrum of a Duck, *Anas boschas*. (After Shipley and MacBride.) 1. Ilium. 2. Ischium. 3. Pubis. 4. Pectineal process, the rudiment of the prepubis corresponding to the pubis of the Lizard. 5. Acetabulum. 6. Ilio-ischiatic foramen. 7. Fused vertebrae. 8. Facet on which the projection on the femur, the trochanter, plays. *E.*, The breastbone and shoulder girdle of a rabbit, seen from below and somewhat from in front. (After Borradaile.) *acr.*, Acromion; *cl.*, clavicle; *cor.*, coracoid process; *cp.*, capitulum; *g.c.*, glenoid cavity; *mb.*, manubrium; *mcr.*, metacromion; *sc.*, scapula; *str.*, sternal portion of a rib; *st.*, 2, st. 6, second and sixth sternbrae; *tb.*, tuberculum; *vr.*, vertebral portion of a rib; *x.*, xiphisternum; *x.c.*, xiphoid cartilage. *F.*, Sternum and sternal ribs of a Dog, *Canis familiaris*. (After Shipley and MacBride.) 1. Presternum. 2. First sternbrae of mesosternum. 3. Last sternbrae of mesosternum. 4. Xiphisternum. The flattened cartilaginous plate terminating the xiphisternum is not shown. 5. First sternal rib.

III. Pectoral girdles of two types of ganoids. *A.*, *Acipenser* (Sturgeon) and *B.*, *Polypterus* (African ganoid). *cl.*, cleithrum; *cv.*, clavacula; *dr.*, dermal rays; *g.*, glenoid surface; *r.*, cartilaginous radialia. (From Kingsley after Gegenbaur.)

size and usurps the function of the clavicle, while the clavicles themselves disappear.

Other bones from the skin may develop, such as the **supracleithra** (post-temporals or supra-temporals). These connect the girdle with the skull; sometimes also post-clavicles and infra-clavicles develop.

A review of the appendicular skeleton, as formed embryologically in the chick and frog, will give one a good idea of the parts as they appear in amphibia. In the reptiles, there is a considerable variation in the shoulder girdle. In the turtle, its position inside the carapace and internal to the ribs is supposed to be due to the fact that the girdle begins its development in front of the ribs, and later sinks to the position it is to occupy in adult life. The scapula, procoracoid, and coracoid are well developed. The median ends of the latter are connected by a cartilaginous epicoracoid. In

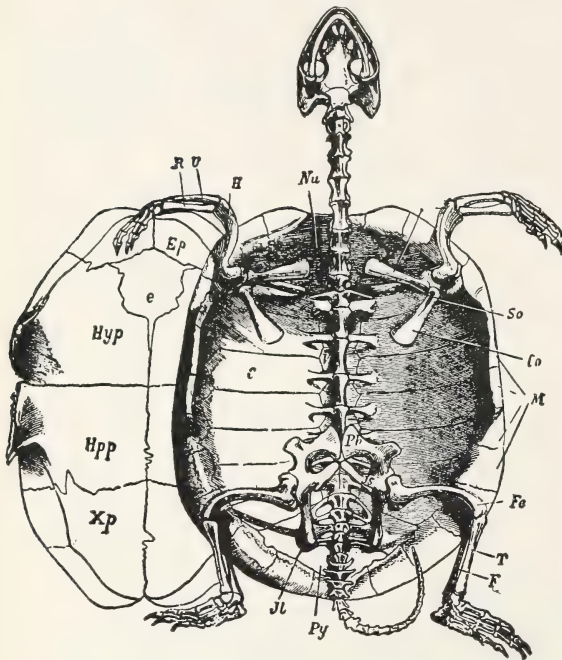


Fig. 417.

Tortoise skeleton *Cistudo luteria*. Ventral side with plastron removed and placed at one side. C, costal plate; Co, coracoid; e, endoplastron; ep, epi-plastron (clavicle); F, fibula; Fe, femur; H, humerus; Hyp, hypoplastron; Hpp, hypoplastron; Il, ilium; Js, ischium; M, marginal plates; Nu, nuchal plates; Py, pygal plates; R, radius; sc, scapula; T, tibia; U, ulna; Xp, xiphi-plastron. (From Parker and Haswell after Zittel.)

other forms of reptiles, the procoracoid usually is reduced and the clavicle takes its place, though in the lizards, the procoracoid still remains in its reduced condition. Clavicles may or may not be present in turtles. If they are, they are represented by the **epi-plastron** (Fig. 417), which is an element of the carapace. In the chameleons and crocodiles the clavicle is entirely lost. In limbless lizards, the girdles are greatly reduced, and in fact in the **Ophidians**, the girdle itself has completely vanished.

In birds (Fig. 418), the scapula is formed as a sword-shaped bar overlying the ribs, while the coracoid extends from the glenoid fossa to the anterior end of the sternum. The procoracoid has entirely disappeared. The two clavicles unite ventrally to form the **wishbone**, called



Fig. 418—Skeletons of Rabbit and Bird.  
A.—The skeleton of a rabbit.

A.—The skeleton of a rabbit.

*acr.*, Acromion; *cd.t.*, condyles for tibia; *cm.*, calcaneus; *cnc.c.*, cnemial crest; *fe.*, shaft of femur; *fb.*, fibula; *g.t.*, greater trochanter; *gr.t.*, premolar and molar teeth; *hm.*, head of humerus; *fit*, fitting into glenoid cavity; *hs.*, shaft of humerus; *is.*, ischium; *mc.*, upper incisor teeth of the left side; *ind.*, lower incisor tooth; *is.*, ischium; *ju.*, jugal bone; *lac.*, lacrymal bone; *mcr.*, metacromion; *mx.*, maxilla; *o.f.*, obturator foramen; *ol.*, olecranon process; *os.*, orbitobasomion bone; *pa.*, kneecap; *pis.*, pisiform bone; *pu.*, pubis; *ra.*, radius; *sc.*, scapula; *sp.s.*, spine of scapula; *st.*, sternum; *st.r.*, sternal ribs; *sup.*, suprascapula; *t.3.*, third trochanter; *ti.*, tibia; *tro.*, trochlea; *ul.*, ulna; *v.cd.*, *v.cer.*, *v.l.*, *v.sac.*, *v.th.*, caudal, cervical, lumbar, sacral, and thoracic regions of the backbone; *v.r.*, vertebral ribs; *x.*, xiphisternum; *x.c.*, xiphoid cartilage; *II*, foramen for optic nerve. The clavicle and hyoid are not shown.

B.—The skeleton of a pigeon, seen from the left side.

*c.r.*, Fixed cervical rib; *c.r.*<sup>1</sup>, free cervical ribs; *cl.*, clavicle; *cor.*, coracoid; *d.*,

the **furcula** (Fig. 418, B.cl.). This may either articulate with the sternum or lie free.

In the monotromes, the shoulder girdle is quite like that of the lizard. This is also true of the young marsupials, but in the adult, it becomes quite like that in all other adult mammals. The coracoid in this instance is reduced to the small coracoid process definitely ankylosed to the ventral end of the scapula. The scapula is well developed with a crest called the **spina scapulae** on its external surface which in turn culminates in an **acromion process** (Fig. 416, II, E, acr.). The clavicle varies with the manner in which the limb is used.

In the higher forms of mammals, the clavicle serves as a strong brace between shoulder and sternum. However, in the ungulates, in the whales, and in a few carnivores it has entirely disappeared. In some mammals it appears as a mere rudiment, without apparent functional value.

Two small cartilaginous elements often intervene between clavicle and sternum, called **episternalia** or **suprasternalia**. Their homologies are unknown.

## THE HIP GIRDLE

The hip, or pelvic girdle (Fig. 419), is quite homologous to the shoulder girdle, the **acetabulum** representing the glenoid fossa. The **ilium** represents the scapula, while **pubis** and **ischium** represent the procoracoid and coracoid. The gap or open space between pubis and ischium is known as the ischio-pubic fenestra. In the lower forms there is another opening, called the obturator foramen, through which the obturator nerve passes to the pelvis. In the higher forms, this usually unites with the ischio-pubic fenestra, the entire opening then being called the **obturator foramen**.

In the lower forms, such as the fishes, the basalia are on the inside, and fused to form a single basal, through which the obturator nerve may pass. The radialia are on its distal surface. The basalia of the two sides do not meet, though there is often a small (or a pair of small) cartilage plates between them. These are supposed to be the homologues of the epipubis of the higher forms. There is no acetabular joint.

In the ganoids and teleosts, ossification begins, but there are no epipubic elements. The pelvic fins may migrate so as to lie in front of the pectoral.

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dentary; *Eu.*, Eustachian tube; *ex.oc.*, exoccipital; *f.r.*, fenestral recess; *fe.*, femur; *fi.*, fibula; *fr.*, frontal; *hu.*, humerus; *i.o.s.*, interorbital septum; *il.*, ilium; *is.*, ischium; *lac.*, lacrymal; *mc.* 1-3, metacarpals; *mt.* 1-4, metatarsals; *n.*, nasal; *o.f.*, obturator foramen; *pa.*, patella; *par.*, parietal; *ph.* 1-4, phalanges; *pl.*, palatine; *pm.*, premaxilla; *p.c.p.*, postorbital process of frontal; *pt.*, pterygoid; *pu.*, pubis; *pyg.*, pygostyle; *q.*, quadrate; *r.c.*, radial carpal; *ra.*, radius; *s.o.b.*, suborbital bar; *s.oc.*, supraoccipital; *sa.*, supra-angular; *sc.*, scapula; *sq.*, squamosal; *st.*, sternum; *st.r.*, sternal ribs; *ti.*, tibia; *u.c.*, ulnar carpal; *u.p.*, uncinate process; *ul.*, ulna; *v.cd.*, caudal vertebrae; *v.r.*, vertebral rib; *x.p.*, xiphoid process; *zy.*, zygomatic process of the squamosal; *I.*, *II.*, foramina for first two cranial nerves; 1-3, first three cervical vertebrae. (From Borradaile.)

The elasmobranchs have a true girdle, although there are no separate elements in it, and it does not ossify, there being but a continuous ischiopubic bar running from one acetabulum to the other with an elongated iliac process running dorsad.

The pelvic girdle lies free of the vertebral column in all fishes, but

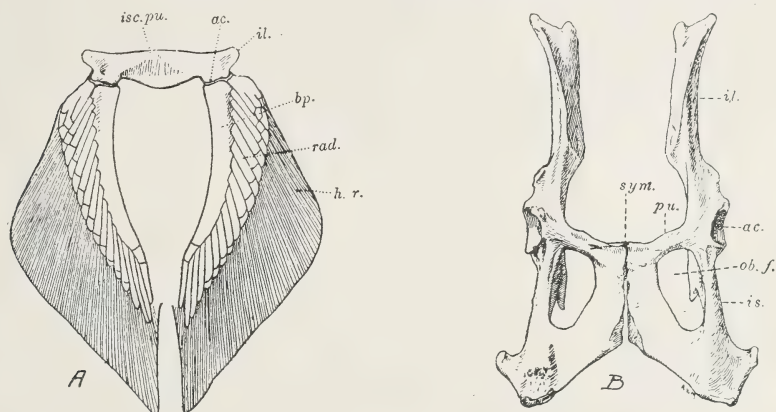


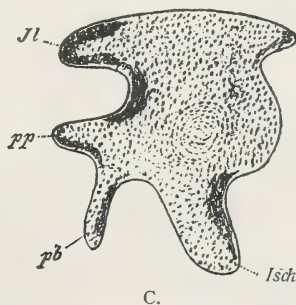
Fig. 419.

A.—The skeleton of the pelvic fins and girdle of a female dogfish.

ac., Acetabular surface; bp., basipterygium; h. r., horny rays; il., iliac process; isc. pu., ischio-pubic region; rad., cartilaginous rays.

B.—The pelvic girdle of a rabbit, from beneath.

ac., Acetabulum; il., ilium; is., ischium; ob. f., obturator foramen; pu., pubis; sym., symphysis pubis. (From Borradaile.)



C.

C.—Anlage of pelvic girdle of 6-day chick embryo to show development.

Il., ilium; Isch., ischium; pb., pubis; pp., pectineal process. (After Johnson.)

in animals that have to support the body-weight upon their limbs, the pelvic girdle becomes definitely attached to the sacrum by the development of one or more sacral ribs.

In the mud puppy (*Necturus*, Fig. 375), the median cartilage extends forward as an epipubic process while from the antero-lateral portion of each pubic bone or cartilage a **pectineal process** extends. In the

salamanders, to the extent of two or three somites, there is a cartilage formed independently of the pubis in the linea alba, called the **ypsiloid cartilage**.

In the frog and other anura, three pelvic bones are present, all of which participate in the forming of the acetabulum. The ilium, however, is very long and the ischio-pubis strongly compressed so that the obturator foramen and ischio-pubic fenestra are absent.

In reptiles, the pelvic bones are more solid and distinct than in any of the lower forms. The ilium is often expanded, the ischio-pubic fenestra large, and the ischium and pubis united from side to side by an epipubic cartilage or a modification of this, known as the **ligamentum medium pelvis**.

In some turtles, the epipubic cartilage bounds the fenestra on the median side, but in all turtles, the fenestra and the obturator foramen are merged into one. In lizards, there may be a separate bone ossified from the posterior part of the epipubis. This bone is called the **os cloacae** or **hypo-ischium**.

In legless lizards, the pelvis is greatly reduced, while all trace of it is lost in the snakes, except the boas and some **opoterodonts** (worm-like serpents). In the crocodiles, due to the oblique position of the pubes, the obturator foramen is very large. The pubes themselves do not unite with each other. There are cartilaginous tips on the medial end which may be separate epipubes. The lower end of the ilium also separates as a distinct bone.

It is interesting to note that the pelvis of **Dinosaurs** has the ilium arranged quite similar to that in birds. The sacrum also is somewhat similar, due, apparently, to the upright position in which these animals walked. The ischia are elongated, extending backward, and often unite below, while the pubic bones extend forward and downward, and have strong post-pubic processes running parallel to the ischium, while often the ilium gives off an iliac spine near the acetabulum.

The **Pteryodactyls** also had elongated ilia similar to the **Dinosaurs**. The ischium was then fused with the ilium so that the pubis took no part in the forming of the acetabulum. The pelvic opening was very small.

In birds of the present time, the pelvic bones are fused, the ilium is quite long, and usually fused with the **synsacrum**, while the ischium and pubis extend backward. The pubes lie in the position of the postpubes of **Dinosaurs** and never meet below, except in ostriches. However, in the embryo, the pubes run forward only to gain their final position later on. There is a pectineal process which arises in the acetabular region and extends forward quite like the pubis in **Dinosaurs**. In the mammals, the obturator foramen and ischio-pubic fenestra are united; all three pelvic bones unite to form the acetabulum, although the ilium and ischium may extend in such a manner as to exclude the pubis from

taking part in the formation of the fossa. Often an **acetabular** or **cotyloid bone** is formed between the ilium and pubic bones, and this may fuse with any of the bones with which it comes in contact.

The inter-pubic cartilage in marsupials and monotremes may or may not persist throughout adult life. When it disappears and the bones unite solidly, but do not definitely ankylose, such union is called a **symphysis**.

In these non-placental mammals (the marsupial and monotremes just mentioned) there are also marsupial bones which first form in cartilage and then extend forward from each pubis in the ventral abdominal wall. Their homology is unknown.

## THE FREE APPENDAGES

In those animals, such as fishes living entirely in the water, the appendages are called **ichthyopterygia**. These are always paired fins. When definite legs or arms are formed, as in all classes of **tetrapoda**, such limbs and their modifications are known as **chiropterygia**. It is commonly supposed that the limbs have developed from the fins, although no one has yet been able to explain the method by which it came about. All explanations, however, assume that certain parts of primitive fins were retained and others likely modified, or, that certain parts were lost, which were originally present, the remaining parts then becoming modified. The lower ganoids have a primitive form of fin, but with increasing complexity, there is a reduction of the basalia either by entire disappearance or by fusion. The remaining ones are then modified so that, in elasmobranchs of the present time, we find the basalia usually number three in the pectoral and two in the pelvic fins, being named from before, backwards, as the pro-, meso-, and meta-pterygium (Fig. 416). The middle one is absent in the hind limbs. The radiales are jointed transversely so as to give more flexibility. If these are arranged entirely on one side of the basalia, they are called **uniserial**, but, if they occur also on the post-axial side, they are called **biserial**. The male elasmobranch has the pelvic fin divided into two lobes, the medial being called the **clasper**, or **mixipterygium**.

The anterior portion of the pectoral fin may develop as a strong defensive spine, sometimes connected with the poison gland. In eels the pelvic fin is lacking.

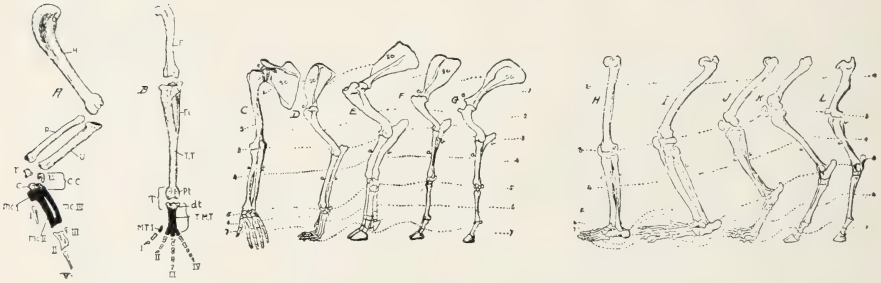
## THE LIMBS

The legs (**chiropterygia**) of all tetrapoda are essentially alike (Fig. 420). Each consists of several regions, comparable in detail with each other. The proximal is the upper arm (**brachium**), or thigh (**femur**), containing a single bone; the **humerus**, or **femur**, in the fore or hind limb respectively. The next region, the forearm (**antebrachium**), or **shank**,



Fig. 420.—Comparisons of fore-limbs and hind-limbs.

1. Wing of a dove; *c.*, carpals; *h.*, humerus; *mc.*, carpo-metacarpus; *p.f.*, primary feathers; *r.*, radius; *s.f.*, secondary feathers; *u.*, ulna.



A, and B.—The fore-limb and hind-limb of a bird compared.

*H.*, Humerus; *R.*, radius; *U.*, ulna; *r.*, radiale; *u.*, ulnare; *C.*, distal carpals united to carpo-metacarpus; *CC.*, the whole carpal region; *MC.I.*, metacarpal of the thumb; *I.*, phalanx of the thumb; *MC.II.*, second metacarpus; *II.*, second digit; *MC.III.*, third metacarpus; *III.*, third digit. *F.*, femur; *T.T.*, tibio-tarsus; *Fi.*, fibula; *Pt.*, proximal tarsals united to lower end of tibia; *dt.*, distal tarsals united to upper end of metatarsus, forming a tarso-metatarsus (*T.M.T.*); *T.*, entire tarsal region; *MT.I.*, first metatarsal, free; *I-IV.*, toes.

*C, D, E, F, G.*—Anterior limb of man, dog, hog, sheep, and horse; *Sc.*, Shoulder-blade; *c.*, coracoid; *a, b.*, bones of forearm; 5, bones of the wrist; 6, bones of the hand; 7, bones of the fingers.

*H, I, J, K, L.*—Posterior limb of man, monkey, dog, sheep, and horse: 1, Hip-joint; 2, thigh bone; 3, knee-joint; 4, bones of leg; 5, ankle-joint; 6, bones of foot; 7, bones of toes. (A, B, after Thomson, C to L, after Le Conte.)

(*crus*) contains two bones, a **radius**, or **tibia**, on the pre-axial, and an **ulna**, or **fibula**, on the postaxial side. Next follows the **podium**, or hand (**manus**), in front and the foot (**pes**) behind, each consisting of three portions. The **basal podial region**, the wrist (**carpus**), or ankle (**tarsus**), consists of several small bones; the second division (**metapodium**) is the palm (**metacarpus**), or instep (**metatarsus**), and lastly come the fingers, or toes (**digits**), each digit consisting of several bones, the **phalanges**. These separate parts are included in the accompanying table, in which the terms given to the separate elements of the wrist and ankle of man are included.

FORE LIMB (Arm)		HIND LIMB (Leg)	
Upper arm (Brachium)	Humerus = Femur		Thigh
Fore arm (Antebrachium) {	Radius = Tibia		Shank (Crus) {
	Ulna = Fibula		
Naviculare (Scaphoid)	Radiale = Tibiale	Astragalus (Talus)	
Lunatum	Intermedium = Intermedium		
Triquetrum	Ulnare = Tibiale	Calcaneus	
	Centrale <sup>1+2</sup> = Centrale <sup>1+2</sup>	Naviculare pedis (Scaphoid)	
Pisiforme			
Basi-podium Wrist (Carpus) {			Basi-podium Ankle (Tarsus) {
Multangulum majus	Carpale <sup>1</sup> = Tarsale <sup>1</sup>	Cuneiform <sup>1</sup>	
Trapezium			
Multangulum minus (Trapezoides)	Carpale <sup>2</sup> = Tarsale <sup>2</sup>	Cuneiform <sup>2</sup>	
Capitatum	Carpale <sup>3</sup> = Tarsale <sup>3</sup>	Cuneiform <sup>3</sup>	
Hamatum {	Carpale <sup>4</sup> = Tarsale <sup>4</sup>	Cuboides	
	Carpale <sup>5</sup> = Tarsale <sup>5</sup>	(Metapodium)	
Palm (Metapodium) {	Metacarpale <sup>1-5</sup> = Metatarsale <sup>1-5</sup>		Instep {
Fingers (Phalanges)	Digits <sup>1-5</sup> = Digits <sup>1-5</sup>	(Phalanges) Toes	

The basal podial region, which is nearly typical in some reptiles, urodeles (Fig. 421) and man, consists of three rows of bones: a proximal of three bones; a radiale, or tibiale, on the anterior side; an ulnare, or fibulare, on the other; and an intermedium (not shown in the figure) between them. The distal row now consists of five carpales, or tarsals, numbered from the anterior side.

The third row is composed of one or two centrales between the other rows. The **metapodials** (Metacarpals and Metatarsals) and the digits, also numbered from one to five, have in some cases special names. The

thumb (digit 1) is the **pollex**, the corresponding great toe is the **hallux**, while the fifth digit is called **minimus**, the second finger in the hand the **index**, and the fourth the **annulus**.

From this typical condition all forms of chiropterygia—legs, arms, wings—are derived by modification, fusion, or disappearance of parts.

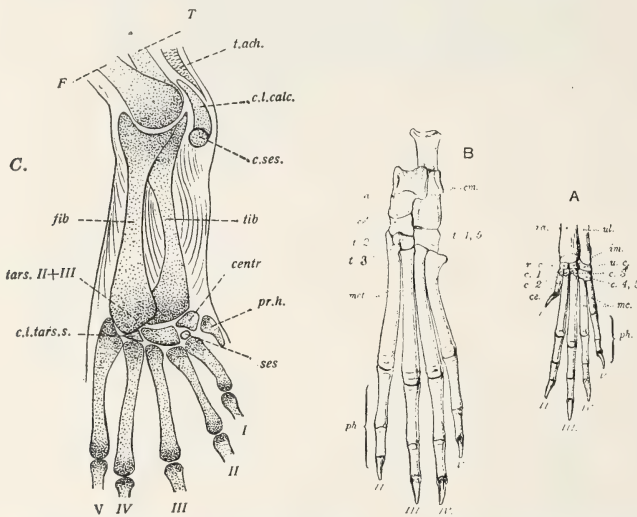


Fig. 421.—The skeleton of the hind-limb of a frog-tadpole compared with the left fore- and hind-feet of a rabbit.

A, fore-foot of rabbit; B, hind-foot of rabbit; C, hind-limb of frog-tadpole shortly before metamorphosis.

In A and B:

a, Astragalus; c.1, first distal carpal or trapezium; c.2, second distal carpal or trapezoid; c.3, third distal carpal or os magnum; c.4,5, fused fourth and fifth distal carpals or unciform; ce., centrale; ce', centrale of hind-foot or navicular; cm., fibulare or calcaneus; im., intermedium or semilunar, mc., metacarpals; met., metatarsals; ph., phalanges; ra., lower end of radius with its epiphysis; r.c., radiale or scaphoid; t.2, second distal tarsal or mesocuneiform; t.3, third distal tarsal or ectocuneiform; t.4,5, fused fourth and fifth distal tarsals or cuboid; u.c., ulnare or cuneiform; ul., lower end of ulnar with its epiphysis; I-V., digits. (From Borradaile.)

In C:

centr., centralis; cl.calc., cartilaginous calcaneous ligament; c.l.tars.s., supplementary cartilaginous tarsal ligament; c.ses., sesamoid cartilage; F, fibula; fib, fibulare; pr.h., prehallux; ses, sesamoid bone; T, tibia; t.ach., tendon of Achilles; tars, II and III, second and third tarsals; tib, tibiale; I-V, phalanges. (After Tschernoff.)

The more distal part is, the more variable it is; reduction takes place on the margins of the appendage, the axial portions being the last to disappear. Occasionally, in various groups (amphibia, mammals) there occur what are interpreted as rudimentary additional digits—prehallux, prepollux, and postminimus—but their status is uncertain. There are also certain membrane-bones developed in the appendages, such as the **patella** (knee-cap) in some reptiles, birds, and many mammals, in the tendon that passes over the knee joint; the **fabellæ** in the angle of the knee of a few mammals, and the **pisiforme** in the carpus of man and some other mammals.

We have already seen that in the frog the radius and ulna, as well as the tibia and fibula, are fused together while the tarsals are considerably elongated. Such fusion is not uncommon in many animals. The extent of fusion varies, however, considerably. In the reptile limb there is an intratarsal joint so that the motion of the foot upon the leg lies between the two rows of tarsal bones, instead of between the tarsals and the bones of the shank. This is quite similar to the condition in birds.

Although limbs are lacking in the snakes and in some of the lizards, nevertheless, there is a considerable increase in the number of phalanges in those reptiles where limbs do occur, while the more proximal bones shorten. In some of the ichthyosaurs there may be as many as a hundred phalanges in a single digit.

The skeleton of pterydactyls shows the fifth digit greatly developed, which forms a definite support for the wings, while the other digits remain more or less normal. In birds the wings are considerably modified (Fig. 420) although the structure is practically normal up to the region of the carpus. The carpal bones are greatly reduced by fusion, while the metacarpals and digits, no matter what their modification, are only three in number.

Embryological studies of the chick show us that, although the first digit begins to develop, it is entirely lost, and the fifth metacarpal, which is present in the embryo, fuses early with the fourth, so that the digital formula is II, III, IV. Then, too, there is an extensive fusion of the bones of the tarsus and foot; the ankle joint is intratarsal, the basal row of tarsal bones fuses with the tibia, while the fibula is considerably reduced to form the tibio-tarsus. The tarsales unite in the same way with the fused metatarsals to form the tarso-metatarsus.

There are hardly ever more than four toes, but the number of phalanges increases from two in digit II, to five in digit V. Ostriches only have two toes, and many other birds three. In the mammals, especially in the higher forms, there is considerable motion of both hand and foot; rotation in the hand is especially noticeable by the motion of the lower end of the radius around the ulna. In the whales the basal part of the forelimb is greatly shortened, while there is considerable multiplication of the phalanges. The hind limb is entirely lacking in some whales, while in others there are two vestigial bones, supposed to be the femur and tibia, imbedded in the muscles of the trunk.

**A supra- or entepicondylar foramen** frequently perforates the inner lower end of the mammalian humerus while in many forms the ulna is fused with the radius in varying degrees. However, the ulna, whether fused or not, always has on its proximal end a strong **olecranon** process which extends beyond the elbow joint for the attachment of the extensor muscles of the forearm.

The earliest prominences for the attachments of the muscles on the femur are known as **trochanters**. They vary from one to three. The

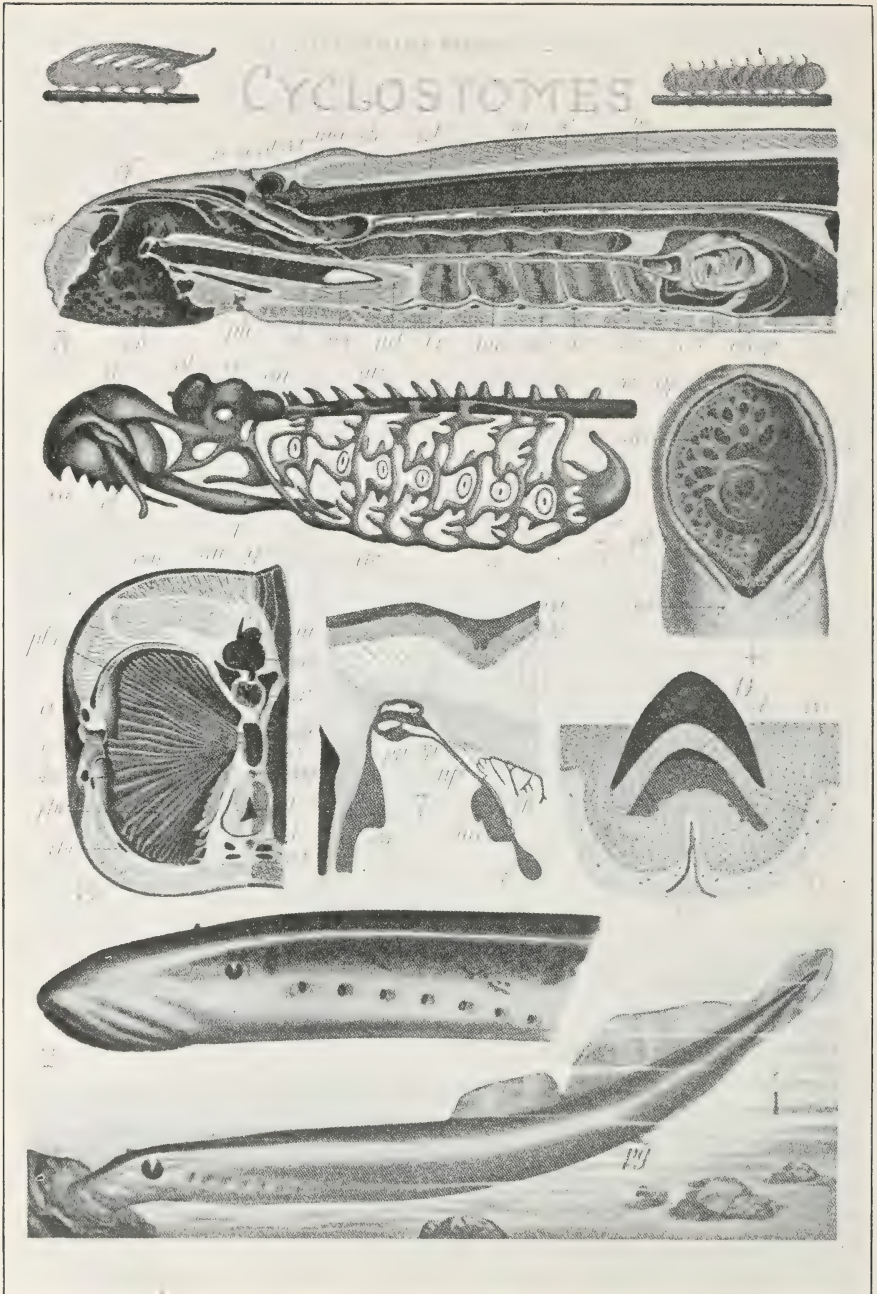


Fig. 422.

Cyclostomes, as exemplified by the marine lamprey, (*Petromyzon marinus*), from 60 cm. to 1 m. long, of European, West African, and North American waters, which goes up stream of the river in spring to lay eggs in the calm waters, and

patella, or knee-cap bone, is analogous to the olecranon process, though it never joins the other bones.

The ankle joint in mammals is never intratarsal, but always between tarsal and crural bones.

Where the bones of the foot rest on the ground as in man and in the bear, such a foot is known as **plantigrade**. Where the toe of the foot includes only the distal phalanges such as in the dog and the cat,

comes down again toward the sea in autumn; and the Planarian Lamprey, (*Petromyzon planari*), from 20 to 30 cm. long which inhabits the calm waters entirely, and is commonly found in rivers.

Fig. 1. A lamprey (*Petromyzon planari*) with its mouth fixed to a rock. *Pg.*, Genital papillae.

Fig. 2. Anterior part of the body of *Petromyzon marinus*, showing the seven branchial openings and the buccal cupping glass surrounded by little papillae. The olfactory opening lies in front of the eye.

Fig. 3. Section through the anterior region of *Petromyzon marinus*. The section, slightly oblique, is nearly sagittal toward the front; it deviates dorsad and downward in order to take in the last of the left branchial sacs; *vb.*, buccal cupping glass; *ca.*, ringed cartilage carrying the principal teeth; *cf.*, cartilaginous pieces of the face; *l.*, lingual sucker, (the posterior part of the sucker has not been taken into the section), is shown surrounded by its sheath; *ml.*, muscles of the lingual sucker; *ph.*, pharynx; *oe.*, oesophagus; *m.oe.*, sphincter closing the entrance of the oesophagus; *a.br.*, branchial aqueduct, showing the seven openings to the branchial sacs; *va.*, valvular apparatus closing the entrance to the aqueduct; *br.-br.*, branchial pockets continuing into the coelomic peribranchial cavities, the one being separated from the other by septa; *C.*, heart; the auricle has been raised partly to show the openings by which it communicates with (1) the ventricle, (2) with the sinus venosus, *sv.*, as one sees them both from behind; *vc.*, entrance of the cardinal veins into the sinus; *j.*, jugular vein; *vh.*, hepatic vein; *tao.*, aortic trunk, with the conus arteriosus and its valvular apparatus at the base of the trunk; *ao.*, aortic roots, reuniting on a level with the fifth branchial opening to form the aorta; *n.*, nostril; *sh.*, bottom of the hypophyseal sac with a valvular sac lying before it; *cer.*, brain; *m.*, medulla; *cd.*, dorsal cord; *f.*, liver; *ov.*, ovary; *p.*, posterior cul-de-sac of the branchial enclosure which protects the pericardium.

Fig. 4. Mouth of the Marine Lamprey. *de.*, teeth of the head of the lingual sucker; *di.*, lower median tooth; *ap.*, principal lateral teeth grouped in twos; *da.*, accessory teeth; *ph.*, sensory papillae of the buccal lip; *os.*, cutaneous sensory organs.

Fig. 5. Anterior region of the skeleton; *ca.*, ringed cartilage carrying the principal teeth; *d.*, *cf.*, cartilaginous parts of the face; *cr.*, brain box; *l.*, lingual cartilage; *ol.*, olfactory capsule; *cd.*, dorsal cord; *an.*, the two neural arches, anterior and posterior, of the same metamere; *cbr.*, branchial enclosure; *a.*, cartilaginous rings surrounding the opening of the external gills; *p.*, posterior cul-de-sac of the branchial enclosure; holding the heart (after Parker); the left half only of the skeleton is represented.

Fig. 6. Section of a horny tooth (odontoid) of lamprey; *ep.*, buccal epithelium; *pa.*, dermal papillae; *D.*, tooth in use; *d.*, replacing tooth, in process of development; *k.*, horn producing cellules. (After Warren.)

Fig. 7. Sagittal section of the Pineal Eye: *ep.*, epidermis; *de.*, dermis; *op.*, pineal eye; *np.*, pineal nerve; *pp.*, parapineal eye; *ha.*, commissure and habenular ganglion; *ch.*, chorioid curtain and lamella concealing the mesencephalon; *ca.*, anterior commissure; on the walls of the thalamencephalon; *cp.*, posterior commissure; *cr.*, cranial cartilage. (After Studnicka.)

Fig. 8. Section of a branchial pocket, passing through internal and external openings. (By reason of the situation of these two openings, the section of the left side of the figure is practically on a plane which places the face to the observer and forms an angle of 45° with the median plane of the animal; the rest of the section, which is only drawn in, is entirely transverse, and therefore seems shortened). *cd.*, dorsal cord; *an.*, neural arch; *m.*, section of the medulla; *g.*, fatty tissue completing the padding of the neural canal; *oe.*, oesophagus and beneath, the aorta; *a.br.*, branchial aqueduct; *tao.*, aortic trunk; *l.*, lingual cartilage and its muscular sheath; *j.*, jugular vein; *cae.*, appendages of the general cavity; *cbr.*, section of the divers pieces of the branchial enclosure; *o.*, internal branchial orifice at the interior of the pocket; *o'*, external branchial opening, with its threefold valves and cartilaginous ring; *a.br.*, wall of the branchial pocket; *fbd.*, branchial leaves; *par.*, peribranchial cavity slightly taken in section; *mu.*, muscles.

(1) Vignettes of the title: Scheme of the respiratory apparatus of two cyclostomes seen from the ventral surface: the oesophagus and the respiratory sacs of the left side (G) only are represented; the horizontal flesh is turned toward the caudal end of the animal; the oesophageo-cutaneous canal, which exists only on the left side is figured in discontinued tracts. To the left the respiratory apparatus of *Myxine* is seen (six branchial pockets with efferent canals running to a single opening) to the right, the respiratory apparatus of *Bellostoma polystrema* (10-14 branchial pockets). (After Dean in Goodrich.) (From the chart of Remy Perrier & Cépède.)

it is called a **digitigrade foot**, while, if the animal, such as the horse or cow, walks upon hoofs which are homologous to the nails on the hands and feet of higher forms, such a foot is called an **unguligrade foot**.

There may be variations and fusions in all these animals. For example, in the horse, it is only the third digit which persists in a functional condition.

## SUMMARY OF THE CRANIUM

### CYCLOSTOMATA

The cranium lies entirely beneath the brain and forms neither side nor roof for the latter (Fig. 422). The cranial cartilages are sometimes said to be homologous with those of the embryonic fish skull.

### DOGFISH

The investing bones are closely applied to the roof and floor of the chondrocranium and modify its form considerably by projecting beyond the cartilaginous part so that apertures and cavities are concealed (Fig. 407). The large **frontals**, which cover the greater part of the roof of the skull, conceal the fontanelles and furnish roofs to the orbits. Immediately behind the frontals is a pair of very small **parietals**; in front of them is an unpaired **supra-ethmoid** to the sides of which are attached a pair of small **nasals**. On the ventral surface is the large **parasphenoid** which forms a kind of clamp to the whole cartilaginous skull-floor; and in front of, and below, the parasphenoid is the **toothed vomer**. Encircling the orbit is a ring of scale-like bones, the **sub-orbitals**.

### PISCES

The fish skull (Fig. 409) is covered above and below by numerous dermal investment bones which are much like those of the primitive extinct amphibia **Stegocephali**. By boiling, all the investment bones are loosened and, when removed, a chondrocranium like that of the dogfish is seen.

In fishes there are primary and secondary structures in the jaw as in the cranium. The primary upper jaw (**palatoquadrate**) is considered homologous with the upper jaw of the dogfish. It does not, however, remain cartilaginous but is ossified by five replacing bones: the **toothed palatine** in front which articulates with the **olfactory capsule**; the **pterygoid** on the ventral edge; the **mesopterygoids** on the dorsal edge of the original cartilaginous bar, and the **quadrate** at the posterior end of the latter: These bones do not enter into the gap and, consequently, do not constitute the actual upper jaw of the adult fish. External to them are two large investing bones, the **premaxilla** and the **maxilla**, which together, form the actual or **secondary upper jaw**. They both bear teeth.

A small scale-like bone, the **jugal**, is attached to the posterior end of the maxilla.

The lower jaw is quite similarly modified. The **articulare** articulates with the quadrate and is continued forward by a narrow pointed rod of cartilage which is really the unossified distal end of the primary **Meckel's cartilage** (the primary lower jaw). The articulare is the ossified proximal end; therefore, a replacing bone. Then there is a large toothed investing bone which ensheaths Meckel's cartilage and forms the main part of the secondary lower jaw. This is the **dentary**. There is also a small investing bone, the **angular**, which is attached to the lower and hinder end of the **articulare**.

The upper jaw connects with the cranium partly by the articulation of the **palatine** with the olfactory region and partly by means of a **suspensorium** formed of two bones separated by a cartilaginous interval. The larger, usually called the **hyomandibular**, articulates with the **auditory capsule** by a facet, and the small pointed **symplectic** fits into a groove in the quadrate. Both bones are attached by fibrous tissue to the quadrate and metapterygoid, so that in this way the suspensorium and palatoquadrate together form an inverted arch which articulates freely in front with the olfactory and behind with the auditory capsule. This gives rise to an extremely mobile upper jaw.

The chondrocranium is a solid one-piece capsule which completely encloses the brain and the principal sense organs. The cranium proper is fused with paired nasal capsules and paired auditory capsules.

Closely associated with the skull, but not fused with it, is the mandibular skeleton, consisting of an upper jaw (**pterygoquadrate cartilages**) and a lower jaw (**Meckel's Cartilage**). Back of the jaw are the visceral arches. These are composed of upper and lower parts like the jaws. The first pair is specialized as the **hyoid arch**, the five others are the more generalized branchial arches that afford support for the gills.

## AMPHIBIA

The skull (Fig. 410) articulates with the **atlas** by two **condyles** which are formed by the **exoccipitals**. There is an **auditory columellar apparatus** fitting into the **fenestra ovalis**.

## AVES

The skull (Fig. 412) is rounded, has large orbits, and the facial bones are extended out upon the beak. The quadrate is movable and articulates with the squamosal. There is a **single occipital condyle**. There are no teeth in modern forms. The cervical vertebrae have paddle-shaped articular surfaces which give the neck great flexibility and thus make the beak a very versatile instrument.

## REPTILIA

The special features in the turtle skull (Figs. 411, 413) are these: Teeth are absent; the maxillary, premaxillary, and dentary bones are covered with hard, chitinous sheaths which form the upper and lower members of the cutting beak; the vomer is a single unpaired median bone, and there are no lachrymals or ectopterygoids. The pterygoids send wings of bone inward. The wings and the palatines form a continuous roof of the mouth; the supraoccipital is prolonged backward into a large, narrow process upon which are inserted the heavy neck muscles. All of these bones, even the quadrate, are firmly united into a solid cranium. There is **only one occipital condyle**.

## MAMMALIA

The skull of the mammal (Figs. 413, 414) is more compact than that of lower forms; consequently, it contains fewer elements than the skull of reptiles. The following reptilian bones are not found in the adult mammalian cranium: pre- and post-orbitals, pre- and post-frontals, basi-ptyergoids, quadrato-jugals, and supra temporals. The lower jaw is reduced to a single pair of bones in the mammal, the angular, splenial, and articulare being absent. The latter bone is often said to have been drawn **in** to form the **malleus** of the ear bonelets, the **quadrate** has been drawn in to form the **incus** bonelet, while a remnant of the hyomandibular cartilage forms the **stapes**. The whalebone whale (baleen whale, Fig. 392), shows the highest type of the so-called **adaptive specialization** among mammals. Here the teeth are rudimentary and functionless though present in the young. In the adult, they are replaced by baleen. The nostrils are paired, the skull symmetrical, the sternum is single, while the ribs are one-headed and articulate only with the transverse processes of the vertebrae.

## SUMMARY OF THE SKELETAL SYSTEM

### THE DOGFISH

The vertebrae develop at the intersection of the myosepta with the mesenchyme that surrounds the notochord and neural tube. Each individual vertebra is formed by the union of the two caudal halves of the two sclerotomes of one segment with the cephalic halves of the two sclerotomes of the next succeeding segment (Fig. 305). The vertebrae therefore alternate with the myotomes.

As the vertebrae and ribs are first formed in cartilage produced by the activity of mesenchyme, so also, bones which form later are true cartilage bones. In the elasmobranchs, the entire skeleton is made up of cartilage with only a slight impregnation of calcareous matter.

Each vertebra begins as four pair of cartilages (called **arcualia**)

which surround the notochord. Dorsally these are an anterior pair of basidorsals and a posterior pair of interdorsals. Ventrally there is an anterior pair of basiventrals and a posterior pair of interventrals.

In some fish and in extinct **Amphibia** and reptiles, these cartilages remain more or less separate. In most vertebrates, however, parts are lost, while the remaining portions fuse together to form a single vertebra which is then composed of a centrum (which encloses the notochord); a dorsally directed neural arch (which encloses the spinal cord); and a haemal arch (enclosing the blood vessels). (Figs. 352, 404.)

The neural arch is made up of the fused basidorsals and the haemal arch of the fused basiventrals, while the centrum develops from varying parts in different groups of animals.

In the elasmobranchs, the centrum is formed within the notochordal sheath. Thus is formed a **chordal centrum** as contradistinguished from that of nearly all other vertebrates where the centra are produced by the fusion of certain arcualia to form a **perichordal** or **arch centrum**.

There are two kinds of ribs: those which arise at the intersection of the myosepta with the horizontal skeletogenous septum (true or intermuscular ribs), (Fig. 423, q), and those which arise at the inter-

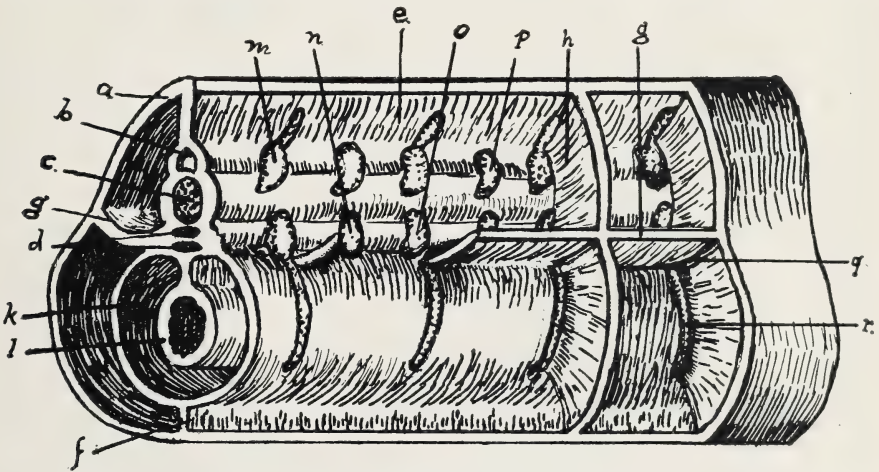


Fig. 423.—Diagram to show the skeleton-forming septa in the trunk region of a vertebrate.

a, skin; b, neural tube; c, notochord; d, blood vessel; e, dorsal skeletogenous septum; f, ventral skeletogenous septum; g, horizontal skeletogenous septum; h, myoseptum; i, epaxial part of the myotome; j, hypaxial part of the myotome; k, coelom; l, intestine; m-p, cartilages from which the vertebrae are formed; m, basidorsal; n, interventral; o, basiventral; p, interdorsal; q, intermuscular rib; r, subperitoneal rib. Note the positions of the vertebral cartilages and ribs with respect to the skeletogenous septa (From Hyman after Goodrich.)

section of the myosepta with the ventral skeletogenous septum or its derivatives (false or subperitoneal ribs), (Fig. 423, r). Teleosts develop the latter type, while all other vertebrates develop true ribs.

Some fishes (such as trout, salmon, herring and polypterus), how-

ever, develop both types of ribs and even additional ones at various levels of the myosepta.

The vertebrae are connected with each other by a strand of notochordal tissue that perforates all the vertebrae like the string through a chain of beads.

The fins have ray-like supports of cartilage, and the pectoral and pelvic limb-skeletons are supported upon simple horseshoe-shaped pectoral and pelvic girdles, each composed of a single piece of cartilage.

## AMPHIBIA

A short cervical and sacral region appear in **Amphibia**, the cervical becoming longer in the higher forms of vertebrates. The pelvic girdle lies free in fishes, but in all other vertebrates it is immovably attached to the sacrum. Three fingers develop early in the amphibian foot although a fourth appears quite late in development (Fig. 421). This fourth finger lies well down on the ulnar side of the hand. Then a rudiment of the fifth (the little finger) appears as a mere bump. The thumb, index, and second finger, therefore, seem to be phylogenetically the oldest digits. This is important in connection with the loss of fingers in other vertebrates, as the last to develop is usually the first to be lost. In the amphibian we find feet instead of fins. This brings a change in the type of movements in the animal, for with fins, an animal can only paddle backwards and forwards. The muscles are, therefore, decidedly different, and nearly all trace of the segmental arrangement in them is lost. Animals which live on land are relatively heavier than those which live in water, so there is need of a much more rigid axial skeleton as well as stronger limb girdles, and limb skeleton. This condition is brought about by a more complete ossification of the parts of the skeleton that bear the most weight. Exoskeleton parts also tend to disappear so that in modern amphibia the exoskeleton is entirely absent with the exception of the **Caecilians** where it is rudimentary. In the **Stegocephalians** there is a head armor while the exoskeleton is lacking on the rest of the body. The sternum first appears in amphibia.

## REPTILIA

In reptiles, birds and mamma's the cervical region is longer than that of the **Amphibia** and the trunk region is divided into an anterior thoracic region with long ribs and a more caudal lumbar region with short ribs or with none.

In all vertebrates, rudimentary ribs are usually found on the cervical and sacral vertebrae when these regions are present.

Fossil remains show that there were many more plates and scutes on the turtles of the past than on those of the present. Both longitudinal and transverse rows of elements have disappeared so that the whole

system is now greatly simplified. Most species of turtles today show a certain percentage of individuals with supernumerary scutes and plates. (Fig. 424.)

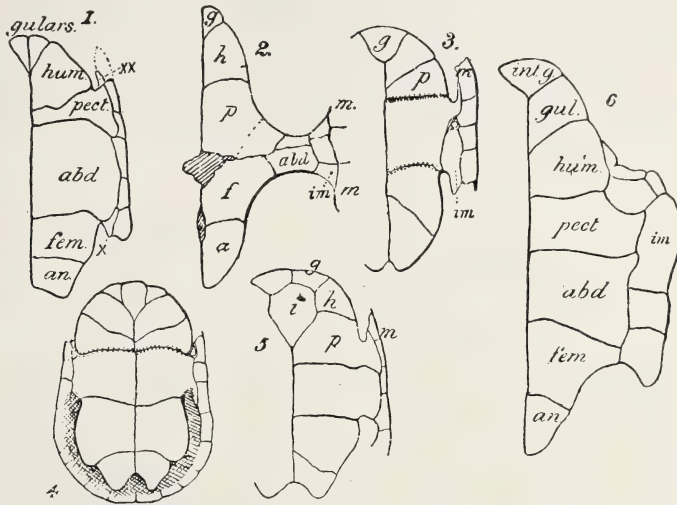


Fig. 424. Various plastra and their horny shields.

1, *Testudo ibera*; 2, *Macrolemmys temminckii*; 3, *Cinosternum odoratum*; 4, *Sternotherus nigricans*; 5, *Chelodina longicollis*; 6, *Chelone mydas*. a or an, anal shield; abd, abdominal shield; f or fem, femoral; g or gul, gular, unpaired in 3; h or hum, humeral shield; i or int.g, intergular; im, inframarginals; m, marginals; p or pect, pectoral; x (in 1), inguinal shield constituting with the axillary xx, the last trace of inframarginals. (After Gadow.)

In the trunk region the vertebrae are rigidly united to the narrow, paddle-like ribs (Fig. 425). There are eight cervical, ten thoracic, two sacral, and a variable number of caudal vertebrae, which are procoelous in form (Fig. 404). A peculiarity of the turtle is that both pectoral and pelvic girdles are inside, instead of outside, the ribs. They actually arise from primordia internal to the ribs so it is not a case of migration. No one has yet been able to give a satisfactory explanation of this fact.

The pectoral girdle (Figs. 416, 417) is made up of a triradiate group of flattened bones: the scapula, the procoracoid, and the coracoid, the last being the largest. These three bones unite to form a socket which receives the head of the humerus. The pelvic arch is more compact. It consists of pubis, ischium, and ilium, which unite to form the acetabulum for the head of the femur. Membrane bones are never found in the pelvic girdle of any animal.

## AVES

The sternum is keeled (Figs. 416, 418), except in such birds as the ostrich, and the ribs have uncinat processes (Fig. 418, B, u.p.) except in **Screamers** (members of the family **Palamedeidae**). The trunk vertebrae

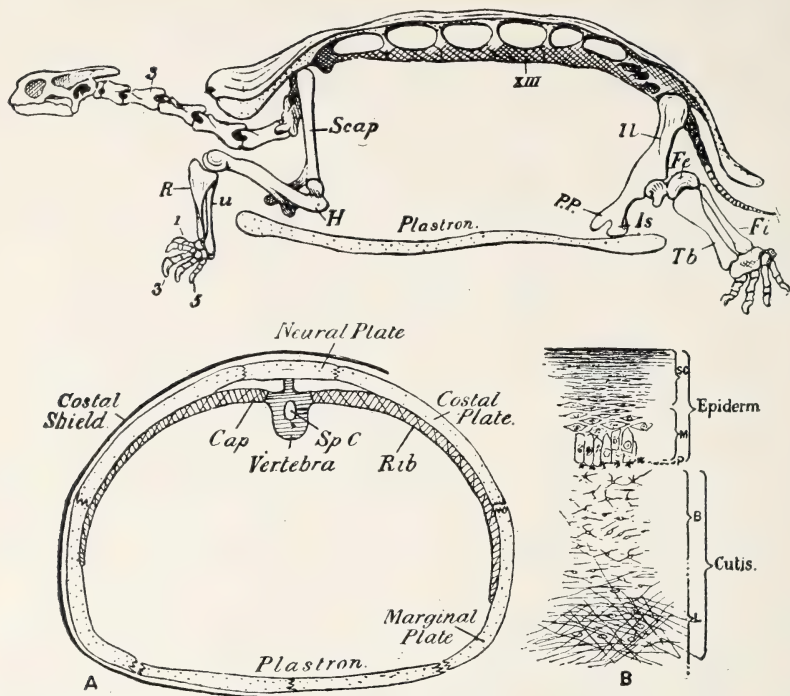


Fig. 425.

A. Diagrammatic transverse section through the shell of *Testudo*. The horny shields have been removed from the right side. On the left side one can see the neural, costal, marginal, and pectoral shields. The bony dermal plates are dotted. *Cap*, capitular portion of rib; *Sp.C*, position of spinal cord.

B. Vertical section through part of the shell, magnified and diagrammatic. *B*, Bony layer of cutis; *L*, leathery layer of the cutis; *M*, cells of the Malpighian layer; *P*, star-shaped pigment-cells; *Sc*, stratum corneum composing the horny shields.

C. Diagram of skeleton of *Testudo elephantopus*, after removal of the left half of the carapace. The plastron is indicated by a section through the middle line. *Fe*, femur, foreshortened; *Fi*, fibula; *H*, humerus; *Il*, ilium; *Is*, ischium; *P.P.*, pubis; *R*, radius; *Scap*, scapula; *Tb*, tibia; *u*, ulna; 3, third cervical vertebra; 1, 3, 5, first, third and fifth fingers; XIII, thirteenth (fifth thoracic) vertebra. (After Gadow.)

are mostly fused. There are three or four pre-caudal vertebrae with terminal **pygostyle** (Fig. 418), two cervical, and three to nine thoracic ribs, the latter attached to the sternum. The pectoral girdle is made up of paired, blade-like **scapulae**, paired **coracoids** which unite with the **sternum**, and three **clavicles** fused in the middle to form the “**wishbone**” or **furcula**. The pelvic girdle is a solid bone, composed of the fused **ischia**, **ilia**, and **pubes**. The pelvis is firmly fused with the sacral vertebrae. The leg skeleton consists of a large **femur**, a slender **fibula**, and a long, stout **tibiotarsus**, made up of the fused tibia and proximal tarsal bones; the ankle joint is between the tibio-tarsus and the tarso-metatarsus.

The foot has four digits of which the hallux usually is directed backward.

**MAMMALIA**

The coracoid portion of the pectoral girdle (Fig. 416) is reduced to a small coracoid process in all placentals while the scapula of all mammals possesses a **spinous process**.

There are usually **paired clavicles** and a median **unpaired interclavicle** in all land mammals. These are membrane bones.

## CHAPTER XXIII

### THE DIGESTIVE SYSTEM

**I**T will be remembered that all multicellular animals pass through a blastula stage, consisting of a hollow sphere composed of a single layer of cells, which then indents to form a gastrula.

This means that there are now two layers of cells where there was only one before. The outer layer is called the **ectoderm** and the inner the **endoderm**. The indented end closes up, leaving a hollow tube composed entirely of endoderm in the center, which, due to its being used for other purposes than the ectoderm, and lying **within** the body, undergoes totally different experiences than does the outer part of the body, and these different experiences modify its structure. This hollow tube is the **primitive digestive tract**. It will thus be seen that the digestive apparatus is the very first one of the various systems of an organism to differentiate.

This distinctive cavity is called the **gastrocoele**. In the lower invertebrates, this gastrocoele remains as a blind cavity with but a single opening. It is among the worms that it first becomes converted into a complete canal by the formation of an anal opening. In animals up to this stage, the same opening serves both for ingestion and egestion.

What is considered a distinct advance in the development of multicellular animals is the development of a **coelom**, or **body cavity**, lying between the digestive tract just mentioned, and the body wall. Up to the time this coelom has developed, the body of the animal consists of a single tube and its wall. But after the coelom has developed, there is established a **secondary** open space **between** the **hollow digestive tube** and the **body wall**.

The coelom is developed by **protrusions**, or **diverticula**, pushing off from the original digestive tube (Fig. 426). This means that the digestive canal of the higher animals only represents a portion of the digestive system of lower animals.

Another departure from the lower organisms consists in the fact that the mouth and anal opening are not developed in the same way in the vertebrates as they are in the lower forms of animals.

In the lower forms, after gastrulation, the **indented end remains open**, thus serving as both mouth and anal opening at the same time. In the higher forms, however, this indented end **closes** so that there is a completely closed hollow tube composed of endoderm on the inside of the body. To form the mouth and anal opening, a new indentation at both the cephalic and caudal ends takes place.

This indentation, coming from the outer layer of the body, means that mouth and anus are composed of **ectoderm** and not endoderm as is the central digestive tube. After the indentation has gone far enough, the thin plate of cells separating the central digestive tube from the mouth and anus breaks through, so that a continuous opening is formed from the mouth through the digestive canal to the anal opening.

All the additional structures that go to make up the digestive system as well as the respiratory system are formed by inpushings or outpush-

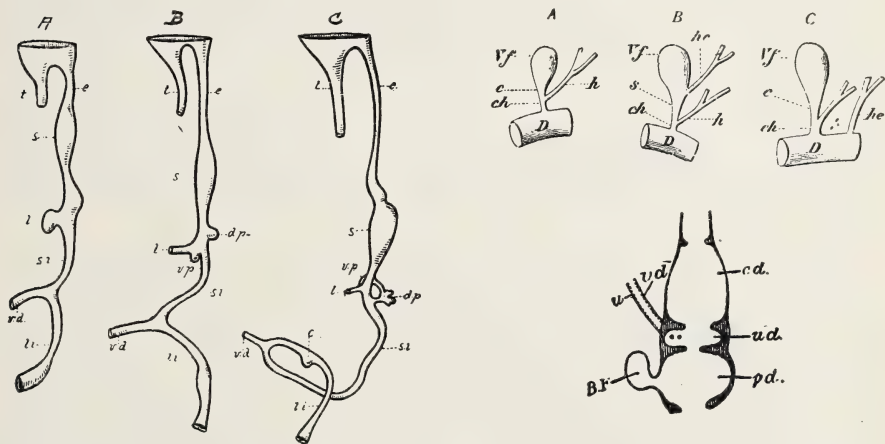


Fig. 426.

I. Diagrams to show method of outpushings in digestive tract. A, 6 mm. pig embryo; B, same at 8 mm.; C, same at 10 mm. *t*, trachea; *e*, oesophagus; *s*, stomach; *l*, liver; *d.p.*, dorsal pancreas; *v.p.*, ventral pancreas; *s.i.*, small intestine; *l.i.*, large intestine; *c*, caecum; *v.d.*, vitelline duct. (From Carey, Journal of General Physiology. Vol. III. No. 1.)

II. Three schematic views of variations in the ducts leading from the gall-bladder. *c* and *s*, cystic duct; *ch*, ductus choledochus; *h*, hepatic duct; *hc*, hepato-cystic duct; *he*, hepato-enteric duct; *vf*, gall-bladder. (From Schimkewitsch after Wiedersheim.)

III. A diagrammatic section of the cloaca of a male bird. (After Gadow.) *cd.*, Upper region of cloaca into which rectum opens; *ud.*, median region into which ureter (*u.*) and vas deferens (*vd.*) open from each side; *pd.*, posterior region into which the bursa Fabricii (*B.F.*) opens.

ings (Fig. 426) of this elementary digestive tract. It will be necessary to remember in one's study of all the higher forms, that no matter how many of these inpushings or outpushings there may develop, and no matter how lengthy the digestive tube may grow and coil, if it be straightened out, it will to all intents and purposes be a continuous hollow tube. The interior of this hollow tube is really **outside** the body in so far as it is subject to all the external conditions to which the body itself is subject. In other words, one may the better understand this if a hollow gas pipe, open at both ends, is thought of. The hollow straight opening, through which the eye can see, represents the digestive canal. The metal of which the pipe is composed represents the walls of the digestive tube. It can, therefore, easily be seen that any con-

ditions, such as dust and moisture, that may be in the atmosphere surrounding the outside of this pipe, will quite likely be found on the inside also.

During the development of the nervous system there is a connection between the lumen of the neural tube and the gastrular mouth so that there is a **temporary connection between the neural tube and the gastrocoele**. This connection is called the **neurenteric canal** (Fig. 328, B, ne.c). This connection, however, soon disappears so that the **gastrocoele is a closed sac** with no opening whatever to the outside of the body **until the mouth and anal openings are pushed in** from the ectoderm as already mentioned.

Definite names are given to the various structures of the growing embryo. The mouth opening is called the **stomatodeum**. The mid portion connecting the mouth with the anal opening is called the **mesodeum**, and the caudal part, which like the stomatodeum is ectodermic, is known as the **proctodeum**.

This does not mean that, in every animal in which an ectodermal mouth and anus has developed, the ectodermal structures take up the same length of the digestive system. In the **articulates** (crustaceans, insects, and spiders) the stomatodeum and proctodeum are much longer and larger proportionately to the mesodeum than in the higher forms of life; in fact, **in the vertebrates, the digestive canal is mainly mesodeal and, therefore, endodermic**. The mouth and anal regions composed of ectoderm are but a small portion of the entire digestive system.

The jaws, teeth, and tongue, which will be taken up separately, do not develop from the simple digestive tube which has just been described; but the other parts of the digestive system, even the most complicated ones, have come from this tube alone by a growing in length, by enlargements of various kinds, by foldings, by outpushings, and by inpushings. Not only have such complex organs as the liver and spleen, thyroid and thymus glands, as well as many others, come from this endodermal tube, but the entire breathing apparatus of chordates has arisen from its cephalic end.

As some chordates, such as fishes, live in water, they require a totally different type of breathing mechanism than those which live on land. Still their **branchial**, or gill, system and the land living **pulmonary** or **lung system** have in each case developed from the same simple digestive tube. It must be remembered that this is only true of chordates. Animals, not chordates, do not show such close relationship between the digestive and respiratory systems.

The intestinal tract, if cut in cross section and examined microscopically, will be found to consist of four layers of **different types** of

cells. Starting from the inner layer we find them in the following order (Fig. 291) :

mucosa

submucosa

muscularia } circular  
                  } longitudinal

serosa

It is in the mucosa or the inner layer that the glands which produce the digestive juices are found. Here, too, are a few scattered involuntary muscle fibers and lymphatic vessels for carrying away the nutriment after it has been changed into a condition so that it can be assimilated.

The submucosa is a thin layer of connective tissue supporting the mucosa.

The muscular layer varies a good deal, but essentially it is composed of two layers of **involuntary muscle cells** both circular and longitudinal, the former lying toward the lumen.

The circular muscles, by contracting, lengthen the intestines, while the contraction of the longitudinal muscles shorten and thicken them. These two actions cause the **peristaltic movement** which occurs during digestion, pushing the food forward and also permitting the various folds and little finger-like projections, called **villi**, to come in contact with all of the material that has been ingested.

In the higher forms, especially in the human being, there are some thirty feet or more of small intestine as contrasted with three or four feet of large. The reason for this can be understood quite readily when it is appreciated that a **two-inch water pipe holds four times as much as a pipe one inch in diameter**. The great mass of material that is ingested is of no value whatever to the animal ingesting it unless such food can be reduced to a more or less liquid state and be absorbed by the mucous lining of the intestinal tract. Digestion, though beginning in the stomach, really takes place in the small intestine. The smaller this intestine is in diameter, therefore, and the more folds the mucosa has, the more readily will the food, after it is sent through the digestive canal, be likely to come in contact with the mucosa and be absorbed.

It is important to understand this as it will throw much light upon various physiological functions of digestion, for, it will be seen that the little finger-like villi must actually do the work of absorbing. That is, after ingested material is ready for absorption, it does not pass by any rule of gravity or mechanics into any definite opening; but these little projections must actually reach out and drink in the necessary material. As these little villi must in turn be kept in good condition and capable of performing their functions by their nerve and blood supplies, it follows that, where the nerve and blood supply is either weakened or lost, the animal may die of starvation regardless of how much food it may ingest.

Many glands are found in the mucosa. Some of the larger ones have pushed their way further and further back so that they have not only passed through the submucosa and muscularia, but have gone far beyond. The liver and pancreas are good examples of those which have left the

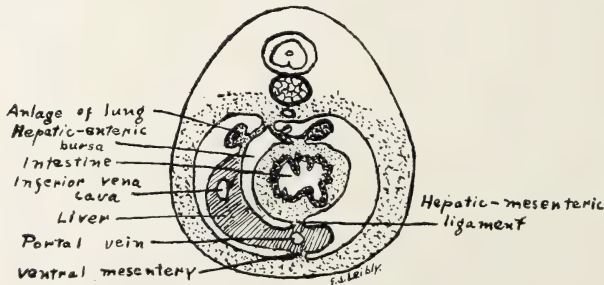
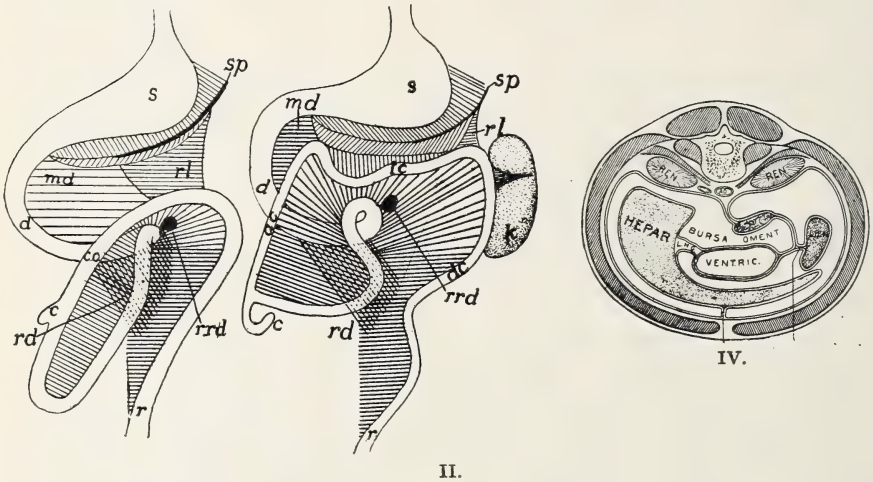
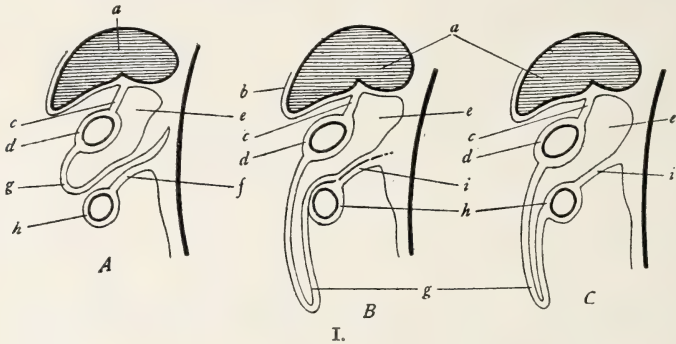


Fig. 427.

I. Diagrams to show formation of greater omentum in mammals and the fusion of the mesogaster and the mesocolon. A, early stage in which the mesogaster is beginning to form a bag at *g*. B, the mesogaster is drawn posteriorly into a

main digestive tract almost entirely but are still connected with it by small ducts.

The glands push their way through both submucosa and muscularia **but**, as they push against the **serosa**, this seems to stretch out ahead of all these outpushings to form a covering for the outgrowths. This is why, not only the liver and pancreas, but every organ in the abdominal cavity is **completely covered by this serous layer**, which, when thought of in its entirety, is called the **peritoneum**.

The kidneys form a single exception to the statement that **all organs** in the abdominal cavity are completely covered by peritoneum. These do not spring from the digestive tract, however, and will be discussed later with the **uro-genital system**.

The entire digestive canal is covered with this serous layer. Figure 427 shows just how this develops and why it is that, while there is a **single layer of serosa over the ventral side** of the intestinal tract, there are **two layers running dorsalward which are attached close to the ventral portion of the spinal region to form the sustaining ligaments**.

Probably this may be made more understandable if the student places an ordinary sheet of paper on the desk before him and lays a pencil at right angles to the long axis of the sheet. By picking up the two ends of the paper so that the pencil is held within the fold, it will be seen that **under the pencil there is only one layer of paper but above it there are two**. The various outpushings of the intestinal tract push the serosa before them just as the pencil does the paper in this case.

The two layers running dorsalward from the organ to form the sustaining ligament, are called the **mesentery**. It is **between the two sheets of mesentery that the blood supply of the organ is carried**.

If it be remembered that the digestive tract begins as a single tube, approximately the same length as that of the body in which it grows, and if the various elongations, outpushings, and inpushings are then followed through the embryonic period, considerable light will be thrown upon our understanding of the adult structure (Fig. 428).

One must, however, be wary in comparing different type-forms of animals, as well as animals of the same species at different stages of their development, or there will be little validity in the comparisons.

The **first portions** of the digestive tract to **differentiate** are the

long bag *g* which is the greater omentum; the mesogaster and mesocolon are fusing at *i*. *C*, completion of the fusion of mesogaster and mesocolon at *i*. *a*, liver; *b*, serosa of the liver; *c*, lesser omentum or gastro-hepato-duodenal ligament; *d*, stomach; *e*, lesser peritoneal sac or cavity of the greater omentum; *f*, mesocolon; *g*, portion of the mesogaster which forms the greater omentum; *h*, intestine; *i*, fusion of the mesogaster and mesocolon. (From Hyman after Hertwig.)

II. Scheme of digestive canal and mesenteries in human embryos, 30 and 50 mm. long. *ac*, ascending colon; *c*, caecum; *co*, colon; *d*, duodenum; *dc*, descending colon; *k*, kidney; *r*, rectum; *rd*, recto-duodenal ligament; *rl*, recto-leinal ligament; *rrd*, recto-duodenal recess; *s*, stomach; *sp*, spleen; *tc*, transverse colon. (From Kingsley after Klaatsch.)

III. Transverse section of a salamander embryo in the region of the liver. (Redrawn from Maurer.)

IV. Schematic arrangement to show the development of the omental bursa. (After Corning.) *P*, Pancreas; *Ao*, Aorta; *L.H.G.*, Hepatogastric ligament.

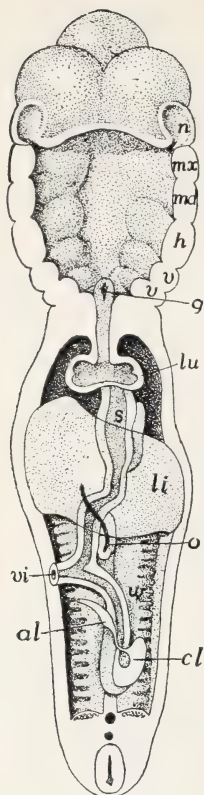


Fig. 428.

Reconstruction of the digestive canal of man. *al*, allantoic stalk; *cl*, cloaca; *g*, glottis; *h*, hyoid arch; *li*, liver; *lu*, lung; *md*, *mx*, mandibular and maxillary arches; *n*, nasal pit; *o*, omphalomesenteric vein; *s*, stomach; *v*, visceral arches; *vi*, vitelline stalk; *w*, Wolffian body. (From Kingsley after His.)

**pharynx** and **stomach**. The former is a funnel-shaped enlargement at the cephalic end with several pairs of lateral diverticula called the **pharyngeal pouches**. These pouches in some animals break through to the outside of the body to form slits (Fig. 295). The stomach may be of many shapes and sizes in the various animals. That portion of the stomach which meets with the oesophagus (the narrow tube connecting pharynx and stomach) is known as the **cardiac** portion, while the caudal opening of the stomach is called the **pylorus** (Fig. 438). It will be found that this pyloric end is rather thick and tough. There is a valve here which closes so that the stomach can be converted into a closed sac. A rather thick short portion of the intestine immediately caudal to the pylorus is known as the **duodenum**. Then follows the **small intestine**, varying in length in all the animals. It ends in the large intestine, and this in turn connects directly with the anal opening to the exterior of the body or in a terminal enlargement which quite often receives the openings of the urinary and reproductive systems before connecting with the anal opening. In the latter case, the thickened portion of the large intestine is called the **cloacal chamber** or, simply, the **cloaca**. (Fig. 426, III.)

In fishes, amphibians, and sauropsida, the cloaca is an important structure. In none of the mammals, except the monotremes, does it appear as a distinct organ.

Various important diverticula of various shapes are thrown out along the digestive tract. The lateral pharyngeal pouches have already been mentioned. In fishes one often finds quite numerous **pyloric caeca**. In mammals at the beginning of the large intestine, where the small one enters it, there are **colic caeca**. In man as well as in several other forms of mammals, one of these little blind sacs is called the **appendix vermiformis**. In birds one finds **cloacal caeca**.

### DETAIL STUDY

The **pharynx** is that open portion behind the nose and mouth in mammals which extends down to the voice box. From there downward (including the **voice box**) the open portion is called the **larynx**.

There are two general types of mouth forms. The first is found in

the great group of **Cyclostomata** (cycle mouths). There are no true jaws (Fig. 422). The mouth is round and cannot be closed. Examples of this form are the **lampreys** and **hagfishes**. This type of mouth is called **suctorial**. The cyclostomata are the only vertebrate parasites known. They attach themselves to a living fish and suck their way directly through the muscles of the host.

The second type of mouth belongs to that group called the **Gnathostomata** (jaw-mouths). This type of animal has movable bones or cartilaginous jaws and usually possesses teeth formed of dentine and underlain with enamel. The jaws are developed from one pair of visceral arches. The teeth are quite similar to the placoid scales of certain fishes which have been modified in various ways. There are two theories held in regard to the **Gnathostomata** or jaw-mouth fishes. First, that the mouth is like that of the cyclostomes, to which the gill arches with their associated teeth have been added; and the second, that this jaw-mouth is a **new opening** which originally consisted of a pair of gill-slits which later became fused in the mid ventral line, the first mouth then being lost. Probably the latter view has more supporters, because in the selachians, where there is supposed to be a more primitive condition, the jaw-mouth is not at the extreme cephalic end of the animal, but on the **ventral side** with a long rostrum extending cephalad to it. Later, in some of the ganoids, this jaw-mouth has a **secondary position** at the very tip or terminal end.

The **pharyngeal pockets** develop from a row of outpushings meeting a similar set of inpushings from the outside (Fig. 295). If the point of contact is broken through, as in fishes, such openings are called **gill-slits**. These are **four to eight** in number, which permanently form a communication between the pharynx and the exterior to allow the escape of water taken in by the mouth for use in breathing.

One or more of these slits appear in the early stages of amphibians and in a few forms persist throughout life. In reptiles, birds, and mammals, there are similar inpushings and outpushings during the embryonic period, but only two or three contact-points ever form openings, and then only for a short time. However, the most anterior of these which appears in the selachians as the **spiraculum** or blow-hole, persists in all higher vertebrates as the **Eustachian tube** and the **greater part of the middle ear**. The other pouches disappear, although cartilages, muscles, arteries, and glands arise in the embryo in connection with these pouches.

Sometimes there is an arrested development so that an open communication persists between the pharynx and the exterior of the jaw either upon one or both sides. This is called a **cervical fistula**. It is supposed to be a **permanent gill-slit** that for some mechanical or chemical reason did not continue growing as it normally should have done.

The nasal cavities in fishes lie above the stomato-pharyngeal cavity

and are unconnected therewith, while in amphibians (Fig. 339) there develops a pair of openings called the posterior-nares, or **choanae**, connecting these two portions by openings in the roof of the mouth. This communication is supposed to be one of the changes which was brought about during the transition from a life of water to a life on land. It allows the ingress and egress of air to the pharynx and then to the lungs without opening the mouth. This action, although harmless for an animal living in water, would soon cause the drying up of the mucous membrane lining the mouth cavity if resorted to in air with anywhere near the same frequency. In the nasal cavities this is prevented at least in part by the small size of the external openings, but still more by the formation of slime glands which produce considerable secretion. Then, too, the waste lacrimal fluid diverted from the eyes to the nose is, in all probability, also of assistance in this respect.

There is a tendency in the pharynx to form diverticula in the median line (Fig. 426), that is, there is here an expansion into large sacs or reservoirs which may, or may not, remain in communication with the pharynx itself. The air-bladders in fish are examples (Fig. 441). While this air-bladder is usually a closed sac filled by gases extracted from the blood, there are a few animals in which one finds a rather small air-duct passing from these air-bladders to the pharynx. In fishes, where this occurs, the animal comes to the surface of the water and makes a snapping or swallowing movement. In the higher forms of animals this develops into the **pulmonary system**, the **lateral sacs being the lungs and bronchia** and the **median duct, the trachea**. The opening of the trachea into the pharynx is called the glottis (Fig. 428), which together with the various cartilages and muscles derived from the visceral system, forms the larynx. While there are always two lungs in lung-breathing animals, there is only one air-bladder in those forms of vertebrates which are not lung breathing. Then, too, the air-sac, or air-bladder, is almost always **dorsal to the pharynx** while the **lungs lie ventral** to it.

The flat plate of bone which forms the roof of the mouth and thus separates the nasal cavities from it, is called the **hard palate**. The soft cover of this bony plate which extends backward beyond the palate is known as the **soft palate** or **velum palati**.

Just as one can easily see the **sulcus** in the median line immediately under the nose, so, in looking into the mouth, a **ridge** will be seen, which is formed right through the center of its roof. As the human being, as well as all of the higher forms of animals, is bilaterally symmetrical, and as different portions of the jaw begin their growth from distinctly separate centers, which then grow toward the midline and unite, one can readily understand not only why a ridge is formed on the roof of the mouth but also why there is a **sulcus** immediately below the nose on the outer upper lip. If, due to a mechanical or chemical obstruction of some kind, the two lateral portions of palate or

upper lip do not meet, a **harelip** and **cleft palate** result.

In some birds the two halves of the palate never unite. In some mammals, such as the cat and dog, the two portions forming the upper lip have not united as well as they have in the human being, and, consequently, a deep median groove called the **philtrum**, remains. This line can be seen to run along the entire **septum** of the nose externally.

Next in order of study come the teeth, tongue, tonsils, glands of the mouth cavity, and glands of the pharyngeal pockets.

## TEETH

There are two types of teeth which have no relationship to each other in their origin. The **true teeth** are akin to placoid scales (Fig. 429). They arise by a calcareous secretion at the junction where **ectoderm** and **mesenchyme** meet and are thus a product of both layers.

The other type comes purely and simply from the cuticle and is formed by what is known as **cornification** or **hardening of the epithelium** (Fig. 422, 6). The parts which have invaginated to form the stomatodeum retain the capacity to form hard structures; consequently, any portion of the mouth-walls may secrete scale substances. It is necessary to appreciate this in order to understand that in the different type of fish and amphibia, teeth of almost any number, size, and shape

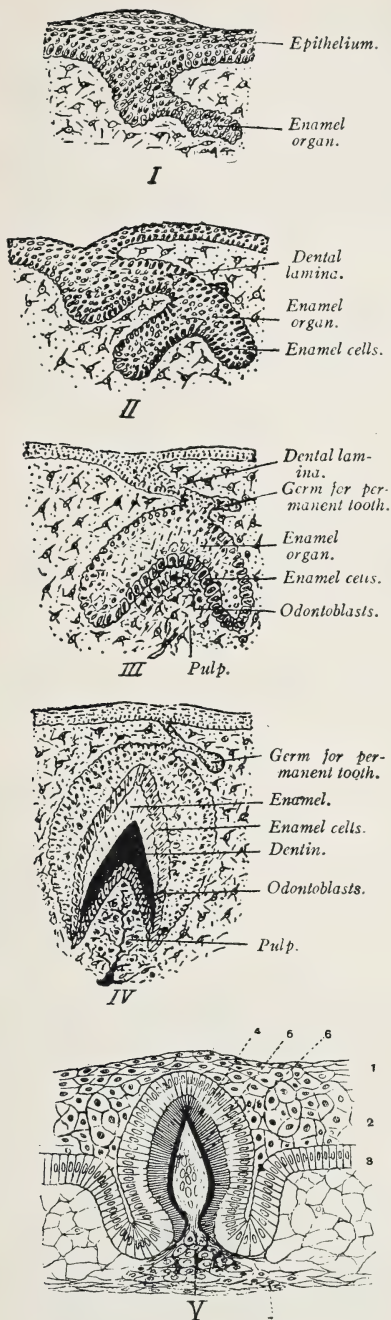


Fig. 429.

I, II, III, IV, Diagrams of developing tooth. (After Hill.)  
V, Section through the skin of an Elasmobranch showing formation of a dermal spine. Highly magnified.

1. Horny layer of ectoderm. 2. Malpighian layer. 3. Columnar cells of ectoderm secreting. 4. Enamel. 5. Dentine (black). 6. Dermal pulp. 7. Connective tissue. (From Shipley and MacBride.)

may be found wherever there is cartilage, or bone, to hold them. In the higher forms of animals, in fact, in all the amniotes, with the exception of some squamata, teeth are found only on the margin of the jaws. Turtles and all present forms of birds are toothless, though many extinct birds, of which fossil remains have been found, did have teeth. It is interesting to note that even in turtles and birds that have no teeth, the **dental ridge** in which the teeth of toothed animals do develop, is nevertheless present in the embryonic stages, it being assumed that this is proof of their descent from toothed ancestors.

It will be observed in Figure 429 that at first the **ectoderm thickens**. The layer of ectodermal cells pushes downward into the mesenchyme. The mesenchymal cells, then, by multiplying rapidly, push portions of this ingrowing plate of cells back up and form a sort of finger-like projection covered by the plate it has pushed before it. The mesenchymal finger-like projection forms the **pulp** of the tooth, while the **plate of cells which covers** it becomes what is known as the **enamel organ**. The pulp forms several layers of cells, the outer ones becoming **odontoblasts**, so called because it is from these that the bone-layer-substance **dentine or ivory** of the tooth is formed. This latter substance is a **secretion** from the **ends of the odontoblasts** and it is this which causes it to be somewhat prismatic in form.

At the base of the enamel organ a denser substance, called **enamel**, is secreted. This fits like a cap over the top and sides of the dentine. The dentine continues to grow and forces the tooth up through the epithelium so that the tip, or crown, then comes into position for use. The nerve supply of the tooth comes from branches of the **trigeminal or fifth cranial nerve**. Both nerves and blood vessels enter through the base of the tooth. Usually, as soon as the teeth are fully formed, the odontoblasts cease growing. However, there are exceptions to this rule. The tusks of elephants and the incisors of rodents function through life and, therefore, continue to grow.

In mammals an additional layer of **modified bone, the cement**, is formed around the root of the tooth. It may even extend through the crown. The teeth in the mouths of skates and some other elasmobranchs are arranged very much like the scales on the surface of the jaw, that is, in groups of five. In most of the vertebrates there is a succession of teeth.

Some animals, such as the shark and turtle, continue to renew and shed their teeth. Such teeth are called **deciduous**.

In mammals, a **second set** of teeth usually arises directly behind or above and below the first set, so that the ends of the second set, which are to force their way through the jaw, push against the roots of the teeth which are already in use.

The group of first teeth formed in man is called the **milk dentition**.

The second is known as the **permanent dentition**. In some mammals, such as the monotremes, sirenians, and cetacea, there is only one dentition; while in some groups there are an indefinite number of successive dentitions. In such animals as guinea pigs, and in some bats, the milk dentition is lost even before birth.

Practically all fishes with few exceptions have teeth, and these extend not only to the lining bones of the mouth but, in some, even to the hyoid and branchial arches. These latter are known as **pharyngeal teeth**.

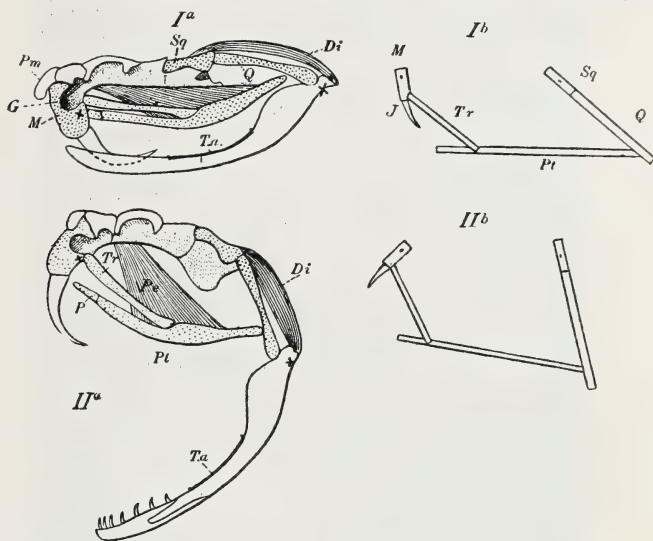


Fig. 430.

Biting mechanism of the rattlesnake. *Ia*, and *Ib*, position of the apparatus when mouth is shut. *IIa*, and *IIb*, position of the apparatus when mouth is opened widely, showing the speno-ptyergoid muscle (*P.e.*) contracted, the pterygoid (*Pt*) pulled forward, the transverse bone or ectopterygoid (*Tr*) pushing the maxillary (*M*) rotating it and thereby causing the poison-fang (*J*) to assume an upright position. *Di*, Digastric muscle, the contraction of which lowers, or opens the lower jaw; *G*, the groove or pit characteristic of the Crotaline snakes; *J*, poison fang; *M*, maxillary; *P*, palatine; *P.e.*, speno-ptyergoid; *Pm*, premaxillary; *Pt*, pterygoid; *Q*, quadrate; *Sq*, squamosal; *T.a.*, insertion of the anterior temporal muscle, by contraction of which the mouth is shut; *Tr*, transversum or ectopterygoid; *X*, origin and insertion of a muscle and a strong ligament, contraction of which draws the maxillary and its tooth back into the position of rest and assists in shutting the mouth. (After Gadow.)

The teeth may be **cone shaped** or **flat**, sometimes they even form large plates as though a number of primitive teeth had grown together. Teeth may be **anchylosed** to the summit of the jaws, attached to their inner side, or have their roots implanted in grooves or pockets as in the human being. The **grooves** in the jaw, in which teeth grow, are called **alveoli**.<sup>1</sup>

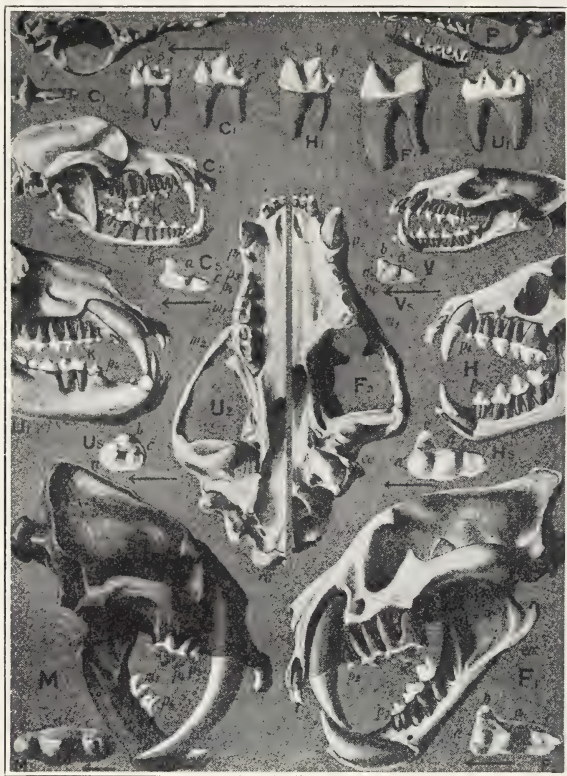
<sup>1</sup>Mammals are said to be **monophyodont** if they develop only one set of teeth, and **diphyodont** if they develop two. However, even in monophyodont mammals, a second set usually develops, although this set later becomes absorbed or remains in a vestigial condition.

When all the teeth are uniform they are said to be **homodont**, while if they vary in shape they are **heterodont**.

Teeth are said to be **acrodont**, if anchylosed to the summit of the jaws, **pleurodont**, if fastened to the jaw's inner side, and **thecodont**, if the roots are implanted in alveoli.

Teeth have also received names according to their function or their peculiar physical appear-

The poison fangs of certain serpents are really specialized teeth on the maxillary bones. They may be permanently **erect or turn as on a pivot** so that when the mouth is closed the teeth lie along the roof of the mouth. Vipers and rattlesnakes are examples of this latter type. (Fig. 430.)



Premolars becoming complicated from before backward, to pointed tuberosities, and compressed laterally (secodont type); the fourth premolar ( $p_4$ ) and the three upper molars united to three tuberosities by sharp ridges. On the lower jaw, these teeth present the entire anterior surface to three pointed tubercles and a flattened posterior heel (Type: tuberculo-sectorial of Cope).

II. *CARNIVORA*. They are distinguished from the Creodonts, from the point of view of dentition, by the differentiation in the two jaws, of a carnassial, or tooth of slicing action, made apparent by its greater development than that of the other molars. It is the 4th premolar of the upper jaw; in the lower jaw it is the 1st molar.

In a general manner, all the teeth placed before the carnassial, that is to say all the premolars, are sharp-pointed; all those which are behind it are tuberculated.

1. *Viverrides* (Civets): The most primitive of the Carnivora properly speaking (true Oligocene), from which all the other forms are usually considered to have been derived. Type shown: *Viverra indica* Desm.

$V$ , skull, seen from the right side. The maxillae have been dissected away sufficiently, as in the other figures, so as to show the roots of the teeth.

$V_s$ , left superior carnassial tooth, seen from the crown.

$V_i$ , left inferior carnassial, seen from the internal aspect.

$$\text{Dental Formula} \quad \frac{3 \quad 1 \quad 4 \quad (3) \quad 2}{3 \quad 1 \quad 4 \quad (3) \quad 2}$$

The number of molars is in general reduced to two, characteristic of a carnivorous specialization.

2. The *Mustelids* (marten, sable, polecat, weasel, stoat) are very close to the primitive type. The carnivorous tendency is strongly developed, as shown by the great reduction of the molars and the higher development of the carnassial tooth.

Starting from the *Viverrides*, the various forms of the carnivora show changes in two clearly divergent directions: one, in which the meat-eating nature of the animal becomes more and more evident, as in *Hyaenidae*, *Felides*, and *Pinnipedes* (seals, eared seals, walruses) and the other which returns somewhat to the omnivorous order, separated from the *Hyaenidae* and *Felides*, and giving rise to the *Canides* and *Ursides*.

3. *Hyaenides*: These form a branch supposedly derived in a direct line from the *Viverrides* (*Hyaenictis*) as they appear in the upper Miocene.

Type Figure: *Hyaena Crocuta* L.

$H$ , the two jaws, seen from the left side.

$H_s$ , left superior carnassial tooth, seen from the crown.

$H_i$ , left inferior carnassial tooth, internal view.

$$\text{Dental Formula} \quad \frac{3 \quad 1 \quad 4 \quad 1}{3 \quad 1 \quad 3 \quad 1}$$

Dentition quite like that of *felides*, and not well developed in a carnivorous sense.

4. *Felides* (cats): The most characteristic of the *Carnivora*. Their most typical representatives appear in the Miocene type, but they are preceded by others, which connect them with the *viverrides*.

Type Figure: The lion (*Felis Leo* L.); *Machairodus cultridens* Cuvier, (a fossil Feline of the European Pliocene age).

$F$ , Skull of a lion, seen from the left side.

$F_s$ , Left half of the same skull, seen from below.

$F_s$ , Left superior carnassial, seen from the crown.

$F_i$ , Left inferior carnassial, seen from the internal aspect.

$$\text{Dental Formula} \quad \frac{3 \quad 1 \quad 3 \quad 1}{3 \quad 1 \quad 2 \quad 1}$$

Of the tuberculated molars, a single one persists, very much reduced ( $m_1$ ). The premolars, although secodont, have undergone a certain reduction in their number as well as in their size, leaving all the functional importance to the carnassials, which have become enormous. The canines are likewise very strong, and are much longer than their neighbors. On the other hand, the incisors, whose cutting function is done much more efficiently by the carnassials, have diminished. The jaw is, all in all, greatly shortened. Notice also the great development and widening of the zygomatic arch, giving a large surface for the levator muscles of the lower jaw (the temporalis, which passes under the arch, and the masseter, which takes its origin from the entire length of the arch). It has thus acquired considerable size and strength. The lower jaw is greatly hollowed out on its external aspect, to permit insertion to the fibers of the large masseter muscle.

$M$ , Skull of *Machairodus cultridens* (extinct saber-toothed tigers), seen from the left side.

$M_s$ , left superior carnassial, seen from the crown.

An exaggeration of the Feline type.

$$\text{Dental Formula} \quad \frac{3 \quad 1 \quad 2 \quad 0}{3 \quad 1 \quad 1 \quad 1}$$

Huge development of the superior canine teeth, which surpass so far those of the lower jaw that they limit closely, on each side, the buccal gap, no longer permitting free use of the canines and carnassials in tearing off meat.

5. *Canides* (dog-like carnivora). A mixed group, both meat-eating and omnivorous. The canides appear early in the Oligocene, their first forms being closely related to the primitive *Viverra* or to the *Creodonts*, some of whose characteristics are even more primitive than those of the typical *Viverrides*. The dog family appears in the early Pliocene.

Type Figure: *Canis familiaris*, L.

$C$ , Left half of the skull, seen from below.

$C'$ , Left inferior maxillary condyle, seen as a horizontal cylinder (characteristic of all the *Carnivora*) in relationship with the glenoid cavity which is hollowed out cylindrically.

$C_s$ , The skull, seen from the right side.

*Cs*, Left superior carnassial, seen from the crown.

*Ci*, Left inferior carnassial, seen from the internal aspect.

Dental Formula  $\frac{3}{3} \frac{1}{1} \frac{4}{3} \frac{3}{3} \frac{(2)}{3}$

6. *Ursides* (Bears). The least carnivorous of all the Carnivora. They originated, apparently, in the upper Miocene, from the primitive *Canides* (*Amphicyon*).

Type Figure: *Ursus arctos* L.

*U<sub>s</sub>*, The two jaws seen from the right side.

*U<sub>i</sub>*, Left half of the base of the skull seen from the lower aspect.

This figure has been placed near the corresponding figure of the Lion in such a manner as to render apparent the comparison between these two extreme types. The comparison must be limited to the portion included in each figure between the incisive teeth and the occipital condyle (*co*). Behind this there is a very large hollowed out area which projects from the posterior aspect, to serve as the insertion of the posterior muscles of the skull and neck.

*Us*, Left superior carnassial, seen from the crown.

*Ui*, Left inferior carnassial, seen from the internal aspect.

Dental Formula  $\frac{3}{3} \frac{1}{1} \frac{3}{2} \frac{2}{3}$

This is probably a regressive adaption to the omnivorous regime. The enormous development of the molars have become quadrituberculated and complicated by the appearance of little tubercles on or between the greater tubercles. Regression of the cutting function of the teeth has followed, the flesh-eating character becoming hardly apparent except in the remarkable power of the upper canines, with their very oblique insertion and long root. The skull also lengthens.

Changes which take place in the Superior Carnassial Teeth: (Figs. *Vs*, *Hs*, *Fs*, *Ms*, *Cs*, *Us*). In the figures the arrow indicates the upper teeth, the arrow's point being directed toward the opening of the mouth.)

*a*, paracone or antero-external cusp; *a'*, anterior accessory cusp; *b*, protocone, or antero-internal cusp; *c*, metacone, or postero-external cusp.

Primitive form (*Viverra*, *Vs*); type trigodont (triconodont). The tooth contains two external cusps (*a*, *c*) compressed laterally and united in a single cutting edge, and a third tubercle (*b*) placed anterior and forward. A fourth tubercle (*a'*) is often found in front of the two external cusps on the same line with them. The cutting edge formed by these last is lengthened in such a manner as to place these tubercles together and thus present three points. The tooth has three roots, two anterior and one posterior.

*Hyænidæ* and *Felides* (*Hs* and *Fs*): The external cutting edge is developed highly in these. The internal anterior tubercle remains conical and blunt, but disappears completely in *Machairodus* (*Ms*).

*Canides*: (*Cs*): Changes in the omnivorous group. The tubercle *a'* has disappeared, the tubercle *b* remaining prominent.

*Ursides*: (*Us*): There is the same type of accentuation as in the *Canides*. Three conical tubercles.

Changes in the Lower Carnassial: (Figs. *Ui*, *Ci*, *Hi*, *Fi*, *Vi*). The arrows are placed above the tooth to indicate the lower ones. The point indicates the anterior direction. *a*, paraconid or antero-internal cusp; *B*, protoconid or external-anterior cusp; *B'*, metaconid or internal posterior cusp; *Y*, hypoconid, or posterior talon.

The primitive type (*Viverrides*, *Vi*) is here the tuberculo-sectorial type of Cope. It contains (1), An anterior part with three tuberculated points; two internal, *A*, *B'*, and one external, *B*, (2) a posterior talon *Y*, low and flattened, carrying one or more blunt tubercles. The tooth presents, in other words, a secodont anterior portion (carnivorous) and a tuberculated posterior portion (omnivorous). It has two roots corresponding to the two parts.

This tuberculo-sectorial type is common to all the lower molars of the creodonts and is limited more or less to the true carnassial tooth in the true Carnivora.

*Canides*, *Ci*: The tuberculo-sectorial type is preserved but with accentuation of the carnassial character. Then there is a reduction of the talon predominance of *B*, reduction of *B'*, and the anterior root is somewhat stronger than the posterior.

*Hyænidæ*, *Hi*: Regression of the talon; the tubercles *A* and *B* compressed and united in a sharp cutting edge, and bicuspid; *B'* notably reduced. The anterior root is much stronger than the posterior.

*Felides*, *Fi*: The talon of *B'* has nearly disappeared and there is predominance of the anterior root.

*Ursides*, *Ui*: Omnivorous type; the secodont part is smooth; its tubercles are blunt and conical; the talon contains more than half of the crown; it is covered by the secondary tubercles, which are elevated almost to the level of the anterior cusps. The whole of the talon has this one surface entirely similar to that of the tuberculated molars which are placed next in position.

Title Figures: *P*, head of Panther (*FELIS*); *Ci*, head of Civet (*VIVERRA*). (From the charts of Rémy, Perrier & Cépède.)

There are four kinds of teeth in mammals (Fig. 431). In the human being, they are alike in both upper and lower jaws as well as alike in both halves of upper and lower jaws. For classification of teeth, we use only one-half of the teeth in either jaw. Thus in man, we find the two teeth nearest the midline—the **incisors**—are followed by a **single canine**. This is distinctly cone shaped and has a single root. Back of this come the **two pre-molars**, commonly called **bicuspids**, having two roots and complicated crowns. They appear both in the milk and permanent den-

titions; and lastly **three molars** quite like the pre-molars in form, with several roots, but appearing only in the permanent dentition. The number and kind of teeth is expressed by what is known as a **dental formula**. As already stated, **the number and kinds of teeth in the two halves of the jaw are the same**, so only one side need be represented in the formula, but, as in some animals the upper and lower jaws do not have the same types and forms of teeth, the formula must take both **upper and lower jaws into consideration**. The upper figures, therefore, represent one-half the upper jaw and the lower figures one-half the lower jaw.

### DENTAL FORMULA

$$i\frac{2}{2}, c\frac{1}{1}, pm\frac{2}{2}, m\frac{3}{3}$$

The foregoing is the dental formula for man; that for the opossum is as follows:

$$i\frac{5}{4}, c\frac{1}{1}, pm\frac{3}{3}, m\frac{4}{4}$$

### EPIDERMAL TEETH

Epidermal teeth occur in cyclostomes (Fig. 422, 6) and various larval stages of amphibia and monotremes. In the cyclostome these are little cone-like projections of cornified epithelium with an underlying core of integument. These epidermal teeth are differently arranged in the lampreys and myxinoids. In the myxinoids they are few, only a single tooth being found on the palate and two chevron-shaped rows on the top. In the lampreys almost the whole inner surface of the oral hood is lined with these teeth of varying shape and there are a varying number upon the tongue. Epidermal teeth are used as a means of fastening the animals to their prey. Those on the myxinoid tongue are used for boring into the fishes on which these parasites feed. In the larval anura (Fig. 318) there are **cornified papillae** serving as teeth along the edge of the jaws. The arrangement varies in different genera. They are frequently aggregated in dental plates which the animal uses in scraping the algae from submerged objects. They are not related to the teeth of cyclostomes.

**Baleen, or whalebone**, should be mentioned here. This is formed in large plates of horny material attached to the margins of the upper jaw (Fig. 392). The fringed ends and edges of these plates serve as strainers to extract the food products from the various materials taken in with the water.

In the embryos of certain lizards and snakes there is a **median tooth** which projects from the mouth and which is used to rupture the egg cell when the young is ready to escape. Such a tooth is called an **egg-tooth**. An egg-tooth is formed in turtles, **Sphenodon**, crocodiles, birds, and monotremes, but in these cases it is only a thick (sometimes calcified) portion of the epidermis.

## THE TONGUE

The tongue varies to a very considerable extent in the different groups of vertebrates (Fig. 432). In mammals the **hyo-branchial support** consists simply of a **basi-hyal** (body) and two pairs of **horns** (cornua). The most cephalad pair are the longer and usually consist of four bony structures, the **cerato-hyal**, the **epi-hyal**, the **stylo-hyal**, and the **tympano-hyal**, the latter bone attached to the skull in the tympanic region. The pair of horns lying caudal consists of only a single skeletal piece of bone known as the **thyro-hyal** which connects the body with the thyroid cartilage of the larynx. In the human being the anterior, or cephalad, horns are considerably modified from those in other mammals.

The tympano-hyal and the stylo-hyal have fused with the **otic region** of the skull to form the **styloid process**, while the hypo-hyal is a mere rudiment connecting with the styloid process by a ligament; the cerato-hyal is not present. The anterior horns, though typically longer and more complex than the others, are called the "lesser" in man, because the earlier anatomists took all of their names from the human being without any comparisons with other forms.

There is **no functional tongue in fishes**, although the material which develops into a tongue in the higher forms is present. This is known as the anterior part of the **hyo-branchial apparatus**. The more cephalic part of this complex apparatus is found in the floor of the mouth cavity. It is naturally shaped according to the jaw outlines which border it. It may even be pushed forward so as to form a slight elevation by the action of the visceral muscles.

In amphibians, where the gill-bearing function has more or less ceased, this region forms the **basis of the tongue** while a fleshy organ of some kind may develop.

In the higher forms of vertebrates **two to four of the visceral arches form the skeletal basis of the tongue**. The **hyoid arch** is the structural foundation to which the muscles of the tongue are attached. Here one usually finds, although there are many varieties, a **median basi-branchial piece**, called the **os entoglossum**, and two caudad projecting horns—the **cornua**. In **Sauropsida** the tongue is a direct condition of this and the principal motion consists in protruding and withdrawing the entire organ by means of the two caudal horns which lie in sheaths from which they may be everted. The tongue is sometimes quite long, and then the sheaths and the enclosed horns are, of course, of corresponding length. If the horns are very long, some disposition must be made of them when retracted. This is interestingly observed in the salamander, **Spelerpes fuscus**, where the sheaths of the horns run down the sides of the body until they are attached to the pelvic bones, the ilia. In the woodpecker they pass around the occipital region over the top of the head and end near the anterior nares of the base of the upper beak. In

such cases the ends of the horns are fastened to the bottom of the sheaths so that the sheath is turned inside out when they are withdrawn.

The tongue develops between the hyoid and mandibular arches (Fig. 432). The hyoid often extends into and supports the tongue. Consequently, the organ itself cannot be moved unless its supporting skeleton is likewise moved. The tongue is a **sensory organ** but can also be used as an **organ of touch and taste**. There are little elevations (Fig. 433) known as papillae, in many if not most animal tongues. Some of these

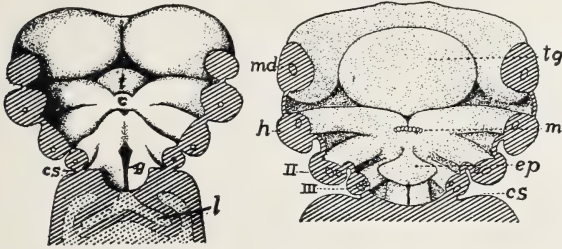


Fig. 432.

Two stages in the development of the tongue and pharyngeal floor of man, *c*, copula (basibyal element); *cs*, cervical sinus; *ep*, epiglottis; *g*, glottis; *h*, hyoid arch; *md*, mandibular arch; *mth*, median anlage of thyroid gland; *t*, tuberculum impar; *tg*, tongue. (From Kingsley after His.)

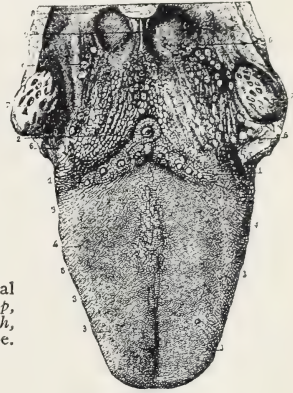


Fig. 433.

Papillary surfaces of the human tongue showing fauces and tonsils. 1, 1, circumvallate papillae, in front of 2, the foramen caecum; 3, fungiform papillae; 4, filiform and conical papillae; 5, transverse and oblique rugae; 6, mucous glands at the base of the tongue and in the fauces; 7, tonsils; 8, part of the epiglottis; 9, median glosso-epiglottidean fold (frenum epiglottis). (From Hill after Sappey.)

are sensory while others have become hardened and serve as rasping organs.

In the cyclostomes the tongue is thick and fleshy and is supported by a cartilaginous skeleton. The muscles which throw out the tongue, are called **protractor muscles**, and those which draw the tongue back to its normal position, are known as **retractors**. These muscles are developed from the **postotic myotomes** and their nerve supply comes from the **hypo-glossal nerve**. In the myxinoids the **terminal end** of the tongue possesses **epidermal teeth** which form a boring organ by which these animals obtain entrance into their prey. In the lampreys, the surface has a rasping organ and also forms part of the sucking apparatus. Among the amphibians there are a few anura (aglossa) in which the tongue is practically absent, but in most cases the tongue actually contains intrinsic muscles supplied by the hypo-glossal nerve when the tongue can be moved quite readily. The tongue of amphibians is made

up of a small basal portion, quite similar to that of the fish, but to this is added a large glandular part which develops between that portion called the **copula, or medial region**, and the lower body. The amphibian tongue secretes slime which is rather useful in capturing its prey. In anura the tongue is fastened to the margin of the jaw, while its free end when not in use lies on the floor of the mouth. In urodeles a much greater portion of the tongue is attached than in anura, for here not only the anterior margin of the tongue but a part of the ventral surface as well, is held quite definitely in place by attachments.

The supporting skeleton of the tongue, as mentioned above, usually consists of two pairs of horns largely formed from the ventral ends of the hyoid and first branchial arches. The median portion, or body, which unites these horns is known as the **copula**. The reptilian tongue includes the parts already mentioned which are found in the amphibia and, in addition, a median growth which arises between the basi-hyal and the lower jaw known as the **tuberculum impar** (Fig. 432, t). Added to this, there is found a pair of **lateral folds** lying above the first visceral (mandibular) arch. From now on, as these parts develop, the **trigeminal nerve sends twigs to the tongue in addition to the hypoglossal and glossopharyngeal as in the lower groups**. In turtles and crocodiles the tongue lies on the floor of the mouth and cannot be protruded. In reptiles possessing a **retractile tongue** the hyoid apparatus extends into that organ. The unpaired cephalic portion, which we have called the **os entoglossum**, is equivalent to the term **copula** or **basi-hyal**; the **retractor** muscles are usually attached to the two horns. In the tongues of birds the lateral parts of the reptilian tongue are not to be found and consequently there is no branch from the trigeminal nerve. It is to be remembered that during the embryological development of a part, the nerves **follow** the growing muscle. The bird's tongue has **no intrinsic muscles**. It has many varieties of form but is usually slender and covered with horny papillae. Even its skeleton is reduced; there is only an os entoglossum with a pair of structural elements attached in front, known as the **paraglossae**, while, on the sides, a pair of horns form the first branchial arch, and, in the median line behind, a portion called the **urohyal** is found. This is well marked in the woodpecker as already stated.

Now we shall discuss the use of the tongue. With the exception of the whale, the tongue is very mobile in all forms of mammalian life. The mobility reaches its extreme in the ant-eaters (Fig. 387). It is largely due to the intrinsic muscles which have been derived to a considerable extent from the hypo-branchial musculature. The tongue itself is developed from the unpaired elevation—the **tuberculum impar**—and from two thickenings on the mandibular arch, which, together with the fleshy ridges above the hyoid arch, form the tongue. These fleshy ridges above the hyoid arch form the back part of the tongue. The line formed

between the anterior and posterior parts cannot readily be seen in the adult, but it is quite close to the **circumvallate papillae** and the **foramen caecum**. This latter is a little open place, or pit, in close relationship to the development of the thyroid gland.

It will thus be seen that the mammalian tongue is quite similar to that of reptiles and exceeds that of birds by having portions in it that come from the mandibular arch.

Two views are usually held as to the relations of the mammalian and amphibian tongues. One holds that the amphibian tongue is entirely unrepresented in the mammals unless it be by the **sublingua**. This is a fleshy fold beneath the tongue of marsupials and lemurs, traces of which occur in other mammals, even in man, as folds (**plicae fimbriatae**) beneath the tongue. In some cases (**Stenops**), the sublingua is supported by cartilage, which may be the entoglossum. The other view is that at least the anterior part of the tongue in amniotes is quite like that of amphibia. This view holds that the **lyssa** (a vermiform mass of cartilage, muscle, and connective tissue, lying ventral to the median septum of the tongue), is the equivalent of the entoglossum and its associated structures.

The dorsal surface of the tongue is covered with a soft epithelium with many mucous glands. There are also varying forms of papillae (Fig. 433), some of which, the **taste buds** for example, are sensory, while some become cornified to form epidermal teeth. A rasping type of tongue in which many of the papillae have become cornified is that of the cat.

## GLANDS

In animals that live under water it is quite natural that comparatively few glands should be found in the mouth cavity other than the very simplest kind. These pour out a slight amount of mucus. If glands were to exist there to any extent, their secretions would be washed away with the incoming and outgoing water that passes through the mouth cavity of such animals. Then, too, one can easily understand that, where a secretion of an animal gland is soluble in water, if such animal lives in water, the secretion could be of no value whatever. Contrasted to this, it can also readily be understood that animals which breathe air must have many glands moistening all surfaces constantly, or the absorption, which is always going on, would soon have all parts of our bodies so dry that they could no longer function. For this reason terrestrial animals have many more secreting glands than water animals.

Mammals, therefore, have **salivary** glands. The saliva, which these secrete, contains not only **mucus**, but a digestive ferment known as **ptyalin** which changes starch into sugar.

Glands are named largely after the **position they occupy**, such as labial, lingual, sub-lingual, etc.

In air-breathing amphibia, snakes, and lizards, there are **labial glands** opening at the basis of the teeth, an **intermaxillary** or **internasal** gland in the septum between the nasal cavities, as well as **palatal** glands near the **choanae**. These latter glands are lacking in the caecilians. There is a sub-lingual gland on either side in many reptiles. Probably all secretions from salivary glands in snakes are poisonous. There is only one known poisonous lizard (**Heloderma**). The sub-lingual glands furnish the poison. Birds do not have labial and internasal glands, but they do have numerous other glands which open separately into the roof of the mouth. They also have anterior and posterior sub-linguals and even sometimes "**angle**" glands at the angle of the mouth, a condition sometimes supposed to be a remnant of the labial glands in the **Sauropsida**. Mammals possess small **labial**, **buccal**, **lingual**, and **palatine** glands imbedded in the mucous membrane of the mouth. Each of these opens through a separate duct. All of these glands serve to keep the various surfaces moist.

Many glands, however, have become **specialized**; for example, the **intermaxillary** glands of frogs and toads (opening into the roof of the mouth) secrete a viscid and sticky fluid which the tongue uses as it is thrown out to catch and hold insects and other moving objects. So, too, the **buccal glands** of poisonous serpents furnish the venom which is sent forth through the poison fangs. These poison fangs, it will be remembered, are **teeth**, and they are provided either with a groove along the external surface or else they have a very small lumen through the center of the tooth and act very much like a hypodermic needle. Those glands, which assist in throwing out a thin watery lubricant, are called **serous glands**, while those assisting in softening and dissolving dry food so that it can be more easily swallowed, are called **salivary glands** without regard to their position.

In mammals the salivary glands are the **parotid**, lying ventral to the ear (swelling up in man when he has **mumps**), the **submandibular** (called **submaxillary** in human anatomy), the **sublingual**, and the **retrolingual**. This last one is closely associated with the submandibular. It is not found in all mammals.

The **serous** glands secrete a clear fluid without any salivary attribute. The **molar** gland of ungulates and the voluminous **orbital gland** of dogs are examples of this type. The orbital glands open into the mouth-cavity close to the last upper molar. The submandibular is found in the lower jaw beneath the mylohyoid muscle. Its duct (**Wharton's duct**) opens near the lower incisor teeth. The retrolingual gland is near the submandibular with its duct opening close to Wharton's. The sublingual gland lies between the tongue and the alveolar margin of the lower jaw. It empties through several ducts. The parotid opens through **Stenson's duct** near the molars of the upper jaw.

## THE PHARYNX

We have already described the pharynx as the cephalic end of the digestive canal lying between the cavity of the mouth and the oesophagus from which the respiratory system develops. It will be described in more detail in our discussion of the respiratory system. But, as there are certain more or less significant organs developed in the pharyngeal region, it may be well to discuss them at this point. These are especially the **thymus** and **thyroid** glands. It is customary to trace the development of these two glands from the cyclostomes upward because the cyclostomes furnish the first (more generalized) stage of development of such glands and thus make it possible to follow up consecutively any so-called advance from a lower developmental type to a higher one. (Figs. 294, 434.)

There are six pharyngeal pockets (except in the cyclostomes) developed on each side. Each of these pockets possesses a dorsal and a ventral recess. It is around these recesses that a group of epithelial cells develops an organ-anlage quite alike in the lower forms. In the higher forms, however, the dorsal group soon forms the **thymus**, and the ventral forms what are called **epithelial corpuscles**.

These thymus-anlagen may separate from the layer where they originated, or they may fuse into a single elongated organ, or they may become constricted in number, the anterior ones disappearing.

In the cyclostomes there are seven anlagen. In the teleosts there are six pharyngeal pockets, but only four anlagen, and these are all the more posterior ones.

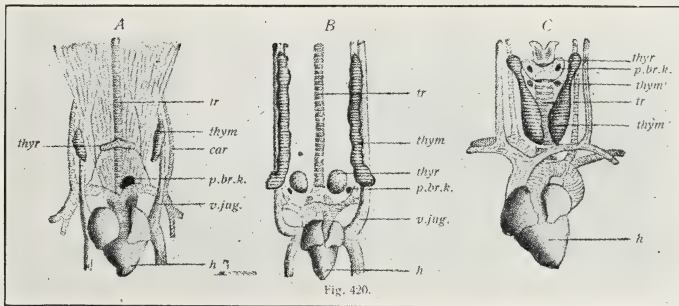


Fig. 434.

Thyroid and thymus glands with closely related organs. A, *lizard*; B, *Hen*; C, *Calf*. *car*, carotid artery; *h*, heart; *p.br.k.*, postbranchial bodies; *thym*, thymus; *thym'*, point of thymus attachment; *thyr*, thyroid gland; *tr*, trachea; *v.jug.*, jugular vein. (After DeMeuron.)

In the mammals it is the third pocket which produces the thymus-anlage, although sometimes there is a tiny addition from the fourth.

The epithelial corpuscles tend to disappear, but in amphibians they become glandular and associate with the carotid artery to form **carotid**

**glands.** The number of these carotid glands varies in different groups of animals.

Immediately behind the last gill slit, in the floor of the pharynx, there is a pair of evaginations. These have been termed **suprapericardial bodies** because they secondarily become associated with the pericardium of the selachians. At present they are usually called **post-branchial bodies**. In selachians a complete pair of these bodies develops but in urodeles and lizards only the **left one** ever completes its development, the right ultimately disappearing. Whether these bodies occur in birds and mammals is not known, although there are somewhat similar growths, called **parathyroid bodies**, which do develop in these animals and then become lost in the lobes of the thyroid gland.

Explanations of these bodies are not yet satisfactory.

The thyroid has come to be considered a very important organ since **endocrinology** looms up so large in the medical world. This gland is an evagination of the pharynx. It is first seen in the selachians but makes its appearance regularly in the higher forms. It arises from the floor of the pharynx at about the level of the interval between the first and second pockets. It becomes compact, and, like the thymus, does not develop a duct. In the larva of **Petromyzon** (one of the cyclostomes) the thyroid appears as an open trough, lined with cilia, which is in open communication with the pharynx, a position quite like that in **Amphioxus**. This trough is called the **hypo-branchial groove**, or **endostyle**, an organ which assists the passage of food down the pharynx by exuding a slimy secretion and by furnishing a definite track, with cilia, which can thus facilitate its movement.

Professor Wilder thinks the thyroid gland is primarily a digestive organ, although in the true vertebrates its structure, as well as its function, has nothing to do with digestion. It is now generally thought that the internal secretions of the thymus gland stimulate growth and inhibit development while the secretions of the thyroid gland stimulate development and inhibit growth.

## THE OESOPHAGUS

This is the swallowing tube connecting the mouth with the stomach. It lies directly against the interior of the dorsal wall of the body-cavity and thus lacks a serous coat. There are no digestive glands in its walls as a rule. Its length quite naturally varies with the length of the neck of the animal in which it occurs. Usually its internal lining is a smooth epithelium. In the chelonians one finds cornified papillae pointing backward. The oesophagus, like other parts of the digestive tract, consists of five layers; however, as it will be remembered that the ectoderm has indented to form the anterior and posterior openings into the digestive tract, a histological examination in the region where these two divisions merge into each other will show a change of structure.

The muscles contained in the walls are striated at the cephalic end and extend back in some cases even into the stomach. The oesophagus usually has the same diameter throughout, but in many, if not most birds, there is a dilation called the **crop** or **ingluvies**. This may either be an expansion on one side, or, as in pigeons, it may consist of a median as well as a pair of lateral chambers. The crop may be a simple reservoir for food, or it may be a real glandular organ where secretions are poured forth and digestion started. In fact, during the breeding season pigeons secrete a milky fluid here, which is used in feeding the young.

### THE STOMACH

The various portions of the stomach have already been named and described in the frog. To the terms there given should be added the **small curvature** at the top or anterior surface of the stomach, usually called the "**lesser**" curvature, and the posterior curvature called the "**greater**."

In some forms of animals, such as amphibians, the lining of the mouth, oesophagus, and stomach is covered with cilia. In birds the stomach is divided into an anterior glandular region, called the **proventriculus**, and a posterior muscular region, called the **gizzard**. After the food has passed through the proventricular region and has mixed with the secretion from its glands, it passes into the gizzard. This latter organ is not only muscular, but the muscles have developed into a pair of disks with tendinous centers. There is a secretion in the gizzard which hardens the lining, and, sometimes, even raises little elevations which are used in grinding the food. One might almost consider them teeth. Remembering that birds have no true teeth, one can readily understand the advantage such an animal has in a gizzard of this type. Grain-eating birds swallow small pebbles which enter the gizzard and are thus also made use of for grinding purposes.

In fact, in the fossil pterodactyl pebbles have been found in such portions as to lead to the supposition that these reptiles had a gizzard. It is well to note in this regard that the grain-eating birds have the best developed gizzards, while birds of prey have gizzards much less fully developed. In one species of pigeons, a part of the wall of the gizzard is ossified. In mammals there are more varying forms of stomachs. These are divided in from one to four regions. The ruminants have two well developed divisions of the stomach (Fig. 435), the **rumen** or **paunch**, and the **reticulum** or **honey comb**, though these two divisions are really enlarged portions of the oesophagus and serve as reservoirs of food. The food is regurgitated into the mouth for mastication and, after it is swallowed a second time, passes into the true stomach, the **psalterium** (also called **omasus** or **manyplies**), and then to the **abomasum** or **rennet**. The latter is used for gastric digestion.

It is of interest here to trace the embryonic changes of the mesentery

in mammals. The mesentery supporting the stomach is called the **mesogastrium**. The first curvature of the stomach, which is toward the left, broadens the corresponding part of the mesogastrium, an effect which is still further increased by the lateral torsion of the entire stomach. The spleen develops within this widened part and by its weight produces a fullness which in turn causes a sagging down behind (dorsal to) the lesser curvature, although attached to the greater. This tendency continues and causes the free lower fold of the bag-like extension to hang down behind the stomach (Fig. 427).

This fold is called the **greater omentum (omentum majus)**, which, as all mesenteries are essentially double, must consist of four layers of serous membranes, applied two and two, each pair holding between them the blood vessels and absorbent vessels naturally belonging to a mesen-

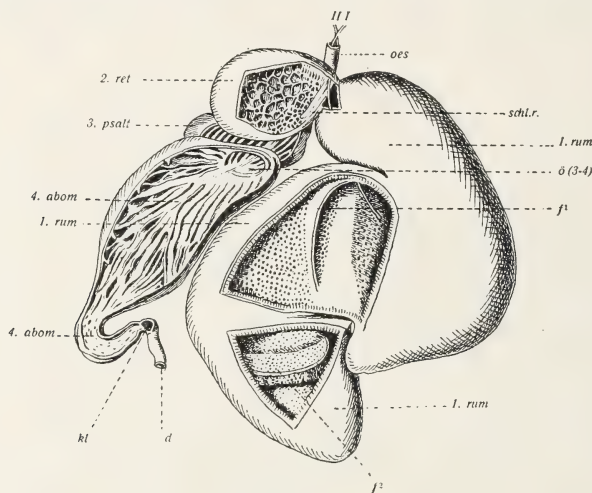


Fig. 435.

Stomach of a Sheep. 4 *abom*, abomasum; *d*, intestine; *f¹f²*, two folds which divide the rumen (paunch) into three regions; *kl*, pyloric valve; *ø* (3-4) opening which leads from the third to the fourth stomach region; *oes*, oesophagus; 3, *psalt*, psalterium (omasus or manyplies); 2, *ret*, reticulum (honeycomb); 1, *rum*, rumen (paunch); *schl.r.*, pharyngeal groove.

The piece of wire marked *I* shows the direction the unmasticated food takes, while *II* shows the direction of the remasticated food. (After Carus and Otto.)

tery. The cavity of the bag is the **lesser peritoneal cavity** of human anatomy, and the opening into it (behind the stomach) is the **foramen epiploicum (foramen of Winslow)**. The bag is widely open in most mammals but in man the foramen is considerably reduced in size and the layers forming the pendulous fold are fused together to form a four-layered apron that hangs below the stomach and covers the intestinal folds.

## THE INTESTINE

The **duodenum** takes its name from the twelve inches of rather large diameter intestine which immediately follows the stomach. The

word "duodenum" is a name which was taken from human anatomy though even in man the structure bearing that name is closer to eleven inches in length than it is to twelve inches in the adult. In the lower forms of animals it varies in length and shape as do all the other parts of the intestinal tract.

Growing from this portion of the intestinal tract, immediately beyond the pylorus, in some of the ganoids and teleosts there may be as many as one to two hundred blind tubes. These are known as the **pyloric caeca**. There are a few elasmobranchs which have only one pair of these caeca. The caeca may be expanded into a pouch called a **bursa Entiana**. The region of the intestine running caudad from the duodenum is also called the **post-hepatic intestine**, so it is in this region caudad to the liver, where most of the digestive processes as well as most of the absorption of the products of digestion take place.

The food, having been more or less mixed with various salivary secretions and having been reduced to a semi-liquid state, receives the bile from the liver and the pancreatic juice from the pancreas (Fig. 436).

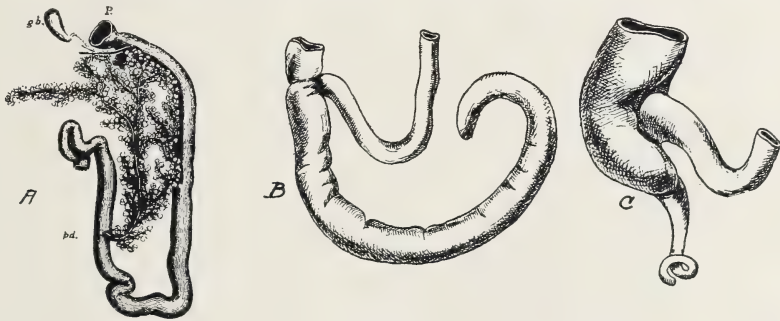


Fig. 436.

A, The duodenum of a rabbit with vine-like pancreas. P., Pyloric end of stomach; gb., gall bladder with bile duct and hepatic ducts; p.d., pancreatic duct. (From Krause after Claude Bernard.)  
B, Appendix vermiformis of kangaroo; C, Appendix vermiformis of human embryo. (After Wiedersheim.)

It is then ready, after being moved back and forth by the peristaltic movement of the intestine, to be taken up and absorbed by the little finger-like processes (villi) which extend from the inner surface of the small intestine. Here it is well to remember that the length of the intestine **varies with the type of food the individual eats**. It is longer in plant-eating animals than in meat-eating animals. A classic illustration of this is the comparative length of the intestine in the adult frog and in the tadpole. The adult frog's intestine is no longer than that of a tadpole half the size a frog would be if it had kept up its relative increase in size.

Any blind pouch in an animal is called a **caecum**. At the beginning of the large intestine where the small intestine enters into it, the joining itself is called the **ileo-caecal junction**, and the little projecting end of

the large intestine is the caecum. It is the tapering end of this caecum which forms the **appendix** (Fig. 436) in man and in some of the other vertebrates. There is also a valve at the junction of the ileum and caecum, known as the ileo-caecal valve.

The first part of the small intestine, which follows the duodenum, is known as the **jejunum**, while the more distal portion is the **ileum**.

Professor Wilder gives the following interesting account of the appendix and succeeding structures:

"At the junction of the small intestine with the large, there is a strong tendency to form one or more **caeca**, or blind sacs, which often become digestive organs of great physiological efficiency. The characteristic form in reptiles is that of a single rather short and wide caecum, symmetrically placed. In birds there are usually two symmetrical ones, which attain great length in scratching birds (e. g., the common fowl), and in ducks and geese, but are quite rudimentary in certain others (woodpeckers, parrots, etc.). Ostriches possess a single caecum of great length (seven to eight meters) and furnished with an internal spiral partition, which greatly increases its effective surface.

"In mammals a single caecum is developed, which varies greatly in size and functional importance. Rudimentary in edentates, most insectivores, and bats, it frequently attains an enormous size in herbivorous or graminivorous forms. In certain rodents (e. g., muskrat, woodchuck), its total capacity equals or exceeds that of the remainder of the alimentary canal, and in the marsupial **Phascolarctus** it is three times the length of the body. In the rabbit it is provided with an internal spiral valve; in certain other rodents and in the higher apes and man, the free end becomes rudimentary, restricts its lumen, and forms a worm-like process, the **processus** (appendix) **vermiformis**, which like all rudimentary organs, is subject to a large amount of individual variation.

"Thus in the human subject the appendix varies in length between the limits of 2-23 cm., the average for an adult being 8-9 cm. It is longest proportionally during fetal life, its length relative to that of the large intestine being 1:10, while in adult life it is 1:20. It is longest absolutely between the ages of ten and twenty, after which it shows a slight reduction. Its status as a rudiment of slight functional value is shown by the tendency toward the obliteration of its lumen, a tendency which increases steadily with age. Furthermore, these two characters, reduction in length and obliteration of the lumen, go hand in hand, short appendices being usually solid, while large ones are likely to possess a lumen.

"The position and arrangement of the colon varies considerably among various mammals. In man it begins low down on the right side, from which there proceed in order an **ascending**, **transverse**, and **descending portion**, connected with the rectum by a **sigmoid flexure**, through

which the tube attains the median line; a similar disposal is seen in many other anthropoids, in lemurs and rodents, the majority of carnivores, and a few others. A more complex condition than this is produced by the formation of long, narrow loops along the course of either the ascending or transverse colons, or both, and these loops may remain simple or roll into spirals. Such **colon labyrinths** are seen in ruminants, in certain rodents as the lemmings and jumping mice, and in a few lemurs.

"From this brief review of the alimentary canal and its modifications the impression is gained that in this array of enlargements, elongations, diverticula, spiral valves, and other devices, we have to do, not with a consecutive anatomical history, but with numerous special cases of physiological adaptations, developed in response to need; and that a similarity in one of these particulars implies, not genetic relationship necessarily, but a similar demand responded to in a similar way. The main object to be achieved in all cases is to regulate the amount of digestive surface to the demands offered by the various kinds of food, and as there is but a limited number of mechanical or architectural devices possible, the same ones are employed in unrelated groups of animals, having arisen independently in response to a similar physiological need. This phenomenon of **parallel development** (or 'analogical resemblance,' as Darwin calls it), may appear in any system or part and has been a frequent source of error in the estimation of the inter-relationship of animals."

It has already been shown that the intestinal tract begins as a straight tube; enlargements then take place in various portions of this tube, the most prominent of such enlargements being the stomach. This enlargement has various paired nerves passing down each side of the digestive canal, prominent among which are the **vagus nerves**. When the stomach has become sufficiently large and extends some distance ventral, it **turns**, so that what was the ventral region now points toward the right side of the individual. This means that any nerves or blood vessels which lie along the right side of the embryonic digestive tract will then lie on the dorsal surface of the stomach and, of course, the left nerves and blood vessels then become ventral. It will save considerable confusion of thought if this be remembered.

### THE LIVER (HEPAR)

The **liver**, as well as the **pancreas** (Fig. 293)—the two largest digestive glands—are derived from the mucosa of the intestine. The former grows by a ventral, and the latter by a dorsal, evagination. These organs are in a sense enlarged intestinal glands which pushed their way through mucosa, submucosa, and muscularia of the intestine. Then, as they pushed against the serosa (which is held down very loosely), this tissue stretched and grew directly ahead of the two glands. The

liver and pancreas are, therefore, covered by a serous membrane, and both are connected on the side from which they pushed forth by a double layer of serosa which forms respective mesenteries. This serous covering is continuous with the covering of the entire intestinal tract and is known as the visceral **peritoneum**. The peritoneum also forms the lining of the abdominal cavity.

The liver is the largest gland in the body but, no matter how many lobes it may develop or how large it may grow, a layer of serosa covers every part of the gland except that part lying toward the side from which it grew. Here, as stated above, the layers coming from each side naturally unite and form the double layer of serosa—the mesentery. The two large **suspensory mesenteries** of the liver are called the **ligamentum hepato-gastricum** (sometimes also called the **lesser omentum**) and the **ligamentum suspensorium-hepatis**.

Practically the entire length of the digestive canal, which passes through the body-cavity, was originally attached by both a dorsal and ventral mesentery. The ventral mesentery, however, becomes lost below the region of the liver, leaving a sharp ventral edge to the two hepatic ligaments.

The function of the liver is to secrete **bile (gall)**, as well as to form various internal products such as **glycogen**, **urea**, and **uric acid**, all of which substances are of great importance to the living animal. The bile is sent to the intestines through the **bile duct** (also called the **choleodochal duct**) while the other products are carried away by the blood. Substances secreted by glands which are not sent through a duct, but carried throughout the body by the blood stream, are known as substances of **internal secretion**.

The liver is a **compound tubular gland**. The many little tubules in the liver which form the gall capillaries empty into the bile duct. This tubular condition of the liver is easily seen in **ichthyopsida** but is difficult to observe in mammals because of the tubular anastomosis and because of the close interrelation of the bile vessels and blood vessels.

The liver begins its growth cephalad at about the same time the blood vessels have already developed into the large **sinus venosus** and **hepatic veins**. These blood vessels also contribute to the **septum transversum** (Fig. 348). The growth of these latter organs prevents the liver from continuing its cephalad growth so that from now on it increases in size in an opposite direction.

Concomitant with its increase in size there is an immigration of mesenchyme between the lobules of the liver. The blood vessels enter at this time. The bile duct (if there are several, this is only true of one of them) has a lateral diverticulum or enlargement. This is the **gall bladder** (Figs. 426, II, 436), which serves as a reservoir for the bile. It may be found in the substance of the liver itself but is usually more or less separate and lies dorsal to the liver substance. It is lacking in some

mammals. In fact, it is not uncommon in man to have the gall bladder removed surgically.

Both the liver and the gall bladder have ducts leading from them. Those coming from the liver are called **hepatic ducts**; those from the gall bladder are called **cystic ducts** (Fig. 436). These unite to form the **common duct** which is also called the **choledochal duct**. It is this common, or choledochal, duct which empties into the intestine. The liver has many and varying shapes in the different animals, depending to a large extent not only upon the shape of the body but on the shape and size of the organs which press upon it. The color of the gall may vary from a brown, yellow, purple, or green, to a vermillion.

### THE PANCREAS

This is the second largest of the digestive glands (Fig. 436) and secretes digestive ferments of great strength, such as **trypsin**, **steapsin**, and **amylpsin**, which digest both proteins and carbohydrates.

In some respects the pancreas resembles the salivary glands and so compensates in part for the absence of such glands in the lower vertebrates. This pancreas arises, as already mentioned, from the dorsal wall of the intestine, close to the liver. There are usually **three diverticula**, one dorsal and two ventral. These latter soon unite. In sharks there is only a single diverticulum, while in the sturgeon there are not only two dorsal but also an equal number of ventral. The proximal portion forms the ducts, the distal, the glands. The number of ducts that persist varies immensely. In some forms of animals all but one disappear, while in the lampreys all may be lost. However, in the mammals two ducts usually persist: the ventral, known as the **pancreatic, or Wirsung's, duct**, and the dorsal called the **accessory, or Santorini's, duct**. Again, the ducts may all remain distinct, or they may unite before they enter the intestines. One of them may even unite with the bile duct. While not absolutely proved, it seems that all vertebrates have some form of pancreas. This may be only a slender tube in the mesentery, as in teleosts, or it may lie outside the muscles in the intestinal walls, as in **dipnoi**. In the **cyclostomes**, it is partly concealed at the insertion of the spiral valve and partly in the liver. In these forms, however, the duct has entirely disappeared so that it forms one of the **ductless glands** or, in other words, a **gland of internal secretion**. The pancreas varies in shape and size. It may be long and straight or possess many lobules. Almost always it is placed between the duodenum and the stomach. There is a question as to whether or not the gland is composed of two separate and distinct structures.

### SUMMARY OF THE DIGESTIVE SYSTEM AMPHIOXUS

The mouth lies at the bottom of a vestibule (Fig. 437) as an **oral funnel** bounded by ciliated **buccal tentacles** with cartilaginous supports

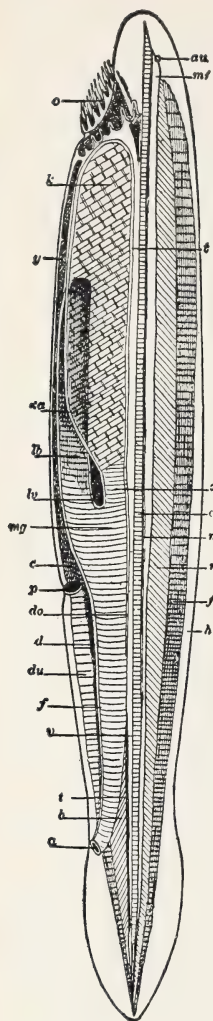


Fig. 437.

*Amphioxus lanceolatus*: a, Anus; au, eye; b, ventral muscles; c, body cavity; ch, notochord; d, intestine; do and du, dorsal and ventral walls of intestine; f, fin-rays; h, skin; k, gills; ka, gill-artery; lb, liver; lv, liver-vein; m<sup>1</sup>, brain vesicle; m<sup>2</sup>, spinal marrow; mg, stomach; o, mouth; p, ventral pore; r, dorsal muscle; s, tail fin; t, t, aorta; v, intestinal vein; x, boundary between gill intestine and stomach intestine; y, hypobranchial groove. (After Hæckel.)

that serve to funnel the water into the pharynx. The mouth is surrounded by a membrane, the **velum**, which acts as a sphincter muscle. A set of **velar tentacles** that serve as a grating to strain out the larger particles is developed on the free edges of the velum.

The **pharynx** has sometimes upward of fifty or more pairs of **gill-clefts** (also called **branchial apertures**) that are separated by partitions in which lie cartilaginous **skeletal rods**, connected across with one another, forming a sort of **branchial basket**. These apertures serve as means of communication between the pharynx and the atrium (the space between the pharynx and the body-wall). The **endostyle** (a longitudinal groove on the ventral side of the pharynx) as well as the **peripharyngeal** and **hyperpharyngeal grooves** all secrete mucus in the form of a continuous rope which carries the food along with it to the stomach. The **atrium** is a sort of mantle composed of folds of the body-wall that enclose the whole branchial apparatus in a voluminous water-filled chamber, the **atrial cavity**. The atrium is lined with ectoderm and has but one opening to the exterior, a posteriorly directed **atriopore**, which carries off the water that comes through the pharyngeal clefts. The atrium is a protection for the delicate pharynx, while the animal is in its sandy burrow, and helps to maintain an uninterrupted current of water.

### ASCIDIANS (TUNICATES)

In the Ascidians (Fig. 313, IV) the method of food concentration and transportation is similar to that of **Amphioxus** although the apparatus, which carries on this function, seems to be of an improved type more appropriate for a sedentary life. An **atrial cavity** surrounds the pharynx which in turn is enclosed by a mantle that surrounds the whole body. A thick **tunic** (after which the animal takes its name) covers this mantle. The **atriopore** is not posterior in direction but lies close to the mouth and is forwardly directed. The stomach opens near the bottom of the pharynx, and the intestine takes a complete turn and opens forward into the atrium. There is

no notochord and no neural tube. Practically none of the structures characteristic of the dorsal side of *Amphioxus* are present.

### FISHES

The mouth opens directly into the capacious pharynx, which is perforated by five gill-slits and the paired spiracles. A short oesophagus of large caliber leads into a U-shaped stomach (Fig. 438), which in turn

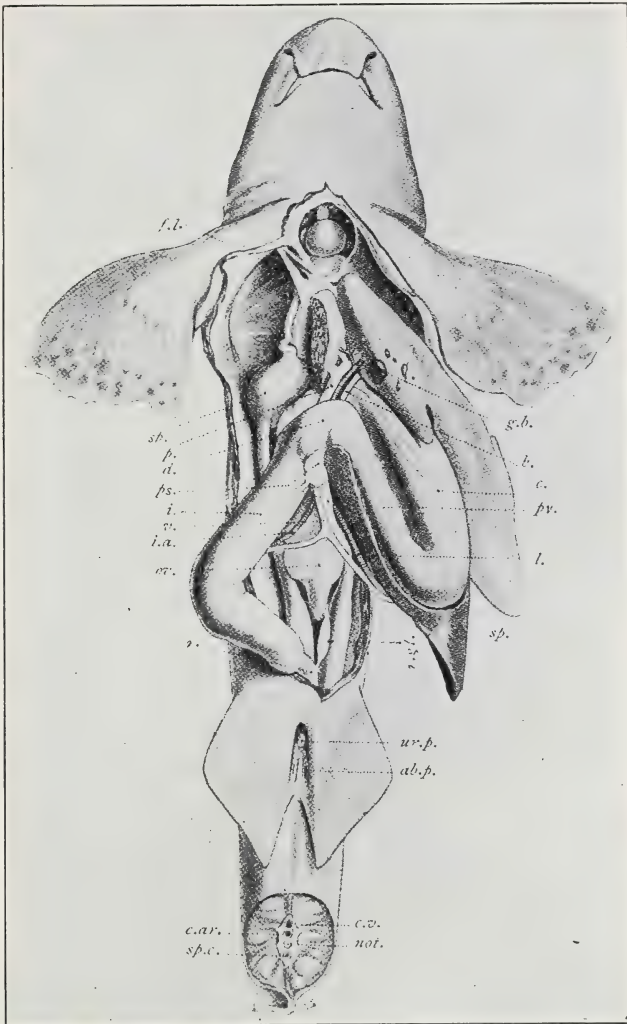


Fig. 438.

A female dogfish in which the abdominal and pericardial cavities have been opened from the ventral side, and the viscera somewhat displaced. The pericardium has been opened slightly to the left of the middle line, and the right lobe of the liver has been cut away.

*ab.p.*, Abdominal pores; *b.*, bile duct; *c.*, cardiac limb of stomach; *c.ar.*, caudal

communicates with the intestine through a valve-shaped opening controlled by a sphincter muscle. The cardiac end of the stomach may end as a blind pouch. The organ is often sufficiently distensible to permit one animal to swallow another as large as itself. The intestine is short but of large diameter and has a secreting surface greatly enlarged by a fold in the shape of a spiral staircase (present, however, in very few **teleostei**) called the **spiral valve**. All primitive fish have this spiral valve. A large bi-lobed liver, which is provided with a gall bladder and a bile duct, opens into the intestine. The pancreas also pours its secretion into the intestine.

## TURTLES

The digestive system of reptiles varies somewhat in carnivorous and herbivorous forms but in all turtles it is comparatively simple. There are no teeth. The tongue is broad and soft and cannot be protruded. The stomach is a simple U-shaped enlargement of the alimentary tract. The intestine is without a caecum; it is clearly divided into large and small intestines. The cloaca is proportionately large.

## AVES

The mouth is hard and narrow and the tongue is hard and often of great functional value. The oesophagus, which has many large cornified papillae, develops an enlargement called the crop. The stomach has a **proventriculus**, which secretes the gastric juice, and a **muscular gizzard** or **gastric mill**. The intestine is U-shaped, and is composed of duodenum, ileum, and rectum. Between the ileum and rectum there are two **caeca**. The rectum opens into a cloaca. There are two bile ducts but no gall bladder. The pancreas empties into the duodenum. The intestine is longer and more coiled than in lower forms. **In cyclostomes, teleostomes, and all non-placental mammals, the intestine terminates in a cloaca**, as do also the urinary and genital ducts. In placental mammals, in cyclostomes, and in teleostomes, the urinary and genital ducts have a distinct and separate opening from that of the intestine.

## MAMMALS

In all vertebrates (except birds and mammals) the coelom consists of the following two compartments:

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artery; *c.v.*, caudal vein; *d*, bursa Entiana; *f.l.*, falciform ligament appearing on surface of left lobe of liver in which it is embedded; *i.*, intestine; *i.a.*, intestinal branch of anterior mesenteric artery; *l.*, lienogastric artery; *not.*, notochord; *ov.*, ovary; *p.*, portal vein lying beside hepatic artery; *ps.*, pancreas with duct opening into intestine; *py.*, pyloric limb of stomach; *r.*, rectum, between hinder ends of oviducts, with rectal gland (*r.gl.*) attached to its dorsal side; *sh.*, right shell gland on course of right oviduct; *sp.*, spleen; *sp.c.*, spinal cord; *ur.p.*, urinary papilla; *v.*, branch of portal vein formed by junction of intestinal and splenic veins.

Besides the above, note—nostrils; oronasal grooves; mouth; pectoral and pelvic fins; pericardial and abdominal cavities; heart, consisting of sinus venosus (behind), ventricle, auricle (showing at sides of ventricle), and conus; cloaca, and transverse section of tail, showing at the sides the myomeres, above the anterior dorsal fin, and in the middle the cartilage of the backbone enclosing spinal cord, notochord, and blood vessels. (After Borradaile.)

- (1) The pericardial cavity which contains the heart only.
- (2) The pleuroperitoneal cavity which contains the other viscera.

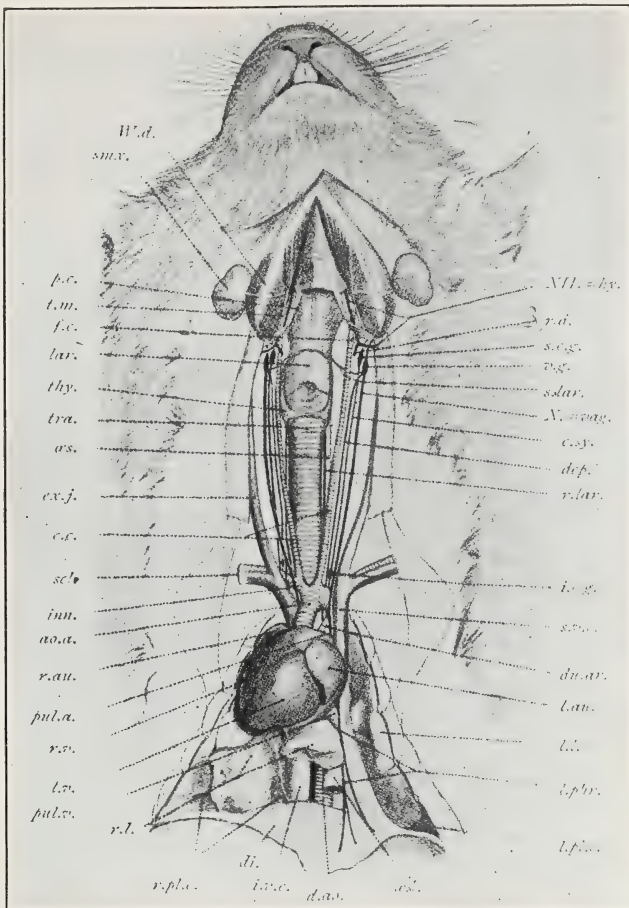


Fig. 439.

A dissection of the neck and thorax of a rabbit. The heart has been displaced a little to the right, and the pericardium removed.

*ao.a.*, Aortic arch; *c.c.*, common carotid arteries; *c.sy.*, cervical sympathetic nerve; *d.ao.*, dorsal aorta; *dep.*, depressor nerve; *di.*, diaphragm; *du.ar.*, ductus arteriosus; *ex.j.*, external jugular vein; *f.c.*, point at which the common carotid divides; *hy.*, hypoglossal nerve; *i.c.g.*, inferior or posterior cervical sympathetic ganglion; *inn.*, innominate artery; *i.v.c.*, inferior vena cava, lying in mediastinum; *l.au.*, left auricle; *l.l.*, left lung; *l.phr.*, left phrenic nerve; *l.pl.c.*, left pleural cavity; *l.v.*, left ventricle; *lar.*, larynx; *œs.*, oesophagus in neck; *œs'*, the same in mediastinum; *p.c.*, posterior cornu of the hyoid; *pul.a.*, pulmonary artery; *pul.v.*, pulmonary vein; *r.au.*, right auricle; *r.d.*, ramus descendens; *r.l.*, right lung, one part bulging into mediastinum; *r.lar.*, recurrent laryngeal nerve; *r.pl.c.*, right pleural cavity; *r.v.*, right ventricle; *s.c.g.*, superior cervical sympathetic ganglion; *s.lar.*, superior laryngeal branch of vagus; *s.v.c.*, superior vena cava; *scl.*, subclavian artery and vein; *smx.*, submaxillary gland; *t.m.*, tendon of mandibular muscle; *thy.*, thyroid gland; *tra.*, trachea; *v.g.*, vagus ganglion; *vag.*, vagus; *W.d.*, duct of submaxillary gland (Wharton's duct); *X.*, *XII.*, cranial nerves. (From Borradaile.)

A partition, the **transverse septum** (Fig. 348), separates the two cavities. In vertebrates lower than **Anura**, the pericardial cavity lies cephalad to the pleuroperitoneal cavity. Beginning with the **Anura**, the pericardial cavity comes to lie ventral to even the cephalic end of the pleuroperitoneal cavity, because the heart and the pericardial cavity descend and carry the transverse septum with them. This descent causes the wall of the pericardial cavity, together with the transverse septum, to form a sac—the pericardial sac—around the heart.

The part of the pleurocardial cavity dorsal to the heart later becomes the pleural cavities.

The pleuroperitoneal cavity in birds and mammals divides into anterior and posterior regions by a partition which descends from the dorsal body-wall to unite with the transverse septum. This partition is known as the **oblique septum** in birds and the **diaphragm** in mammals (Fig. 439). In mammals this diaphragm contains a great amount of striated muscle.

The coelom in birds and mammals has become divided into four compartments: one **pericardial**, two **pleural**, and one **peritoneal cavity**.

While a dorsal mesentery supports the digestive tract in all vertebrates, the ventral mesentery is absent in the adult except in the regions of the liver and bladder.

In mammals, the mesentery of the stomach is prolonged posteriorly to become the greater omentum. An ileo-colic valve and a single caecum are usually found where small and large intestine meet in mammals, although there are a few instances where there are two caeca. In some **edentates**, in bats, in some carnivorous animals, and in many whales, neither valve nor caecum are found.

The caecum in some rodents and marsupials grows as long or longer than the animal's body (it is of great value in digestion here) while in man, it degenerates into the vermiform appendix, the lumen of which tends to close with increasing age.

The intestine and colon in mammals are straight tubes at first but grow into folds later.

In monotremes the rectum terminates in a cloaca, as it does in the **Sauropsida**. This condition also occurs in the young of all mammals, but, in all of these, the urogenital and digestive openings become separated later, and a **perineal fold** develops between the openings.

## CHAPTER XXIV

### THE RESPIRATORY SYSTEM

**I**N the description of the frog it was stated that the trachea and oesophagus have their beginning close together at the caudal end of the pharynx which is also the beginning of the cephalic end of the larynx. In the higher forms of animals, the trachea divides into two **bronchii**. These bronchii again continually subdivide until there are many tiny tubules, called bronchioles, spreading out to all parts of the lungs. These bronchioles form a sort of an air-capillary system through which the inspired air is sent to all parts of the lungs, there to assist in aerating the entire pulmonary blood which has been sent to the lungs, from the heart, through the pulmonary artery. In order that the oxygen in the inspired air can come in direct contact with the blood itself, there must be a rather thin, more or less porous, membrane separating the blood and air.

The lungs, liver, spleen, and kidneys are known as **parenchymatous organs**. It is well to bear this in mind constantly for many diseases find their way from one of these organs to another. A parenchymatous organ is more or less sponge-like and consists of loosely woven tissue in which there are many porous openings. Such organs are invariably supplied with great quantities of blood.

These organs, especially the lungs, have a decidedly thin membrane surrounding the sac-like ends of the bronchioles. In the lungs the oxygen passes through the thin walls to come into direct contact with the venous blood which has been sent there through the pulmonary artery.

What has been said so far regarding the respiratory system applies to vertebrates at large. However, those which live a part of their lives in water have no lungs during that period and in this respect resemble fish and other animals which spend all of their time in the water. In such forms gills (also called **branchiae**) develop on the walls of some of the **visceral clefts** (these are called **gill clefts** (Fig. 295) or **branchial clefts**). The clefts come from the sides of the pharynx and begin as a pair of pouches or grooves of the pharyngeal entoderm. As they then extend toward the sides of the animal they push aside the mesoderm and finally reach the ectoderm. The ectoderm and entoderm then fuse to form a plate. This plate becomes perforated and thus connects the pharynx with the exterior of the body by a number of openings. These openings, or clefts, begin development at the cephalic end and successively continue caudad.

The visceral pouches, although developing in all vertebrates, do not as a rule break through in the mammals. In fact, the pouches may

disappear without leaving any trace whatever, except a **Eustachian tube** and the various ductless glands already mentioned. In the true vertebrates fourteen pairs of these clefts is the largest number found. There are more than this in **Amphioxus** and **Balanoglossus**. In the cyclostomes there are usually seven (eight to seven in notidanid sharks, five or six in teleostomes, and five in birds and mammals). In this numbering, the oral cleft is not included, though there is some evidence that the mouth arose by the coalescence of a pair of gill clefts.

The gill clefts do not form a serial repetition in the same manner as does segmentation in other parts of the body, and it may even be that the metamerism of the head is not of the same character as the metamerism of the gill clefts. In the amniotes where gills are never developed, the branchial pouches, or clefts, however, appear and bear practically the same relation to the aortic and branchial arches as in the lower forms. From this it is often assumed that all of these higher forms which show this relation, have had ancestors with gills.

There is an **interbranchial septum** covered externally with ectoderm and internally with entoderm between every two successive gill clefts. The inner portion of this septum is composed of mesoderm which in its earlier stages contains a diverticulum of the coelom. Later, blood-vessels (aortic arches) and skeletal elements (visceral arches) are developed in each septum. The visceral arches form on the splanchnic side of the coelom and hence are not comparable to girdles or ribs.

In **Cyclostomes** and fishes, the gills are either filamentous or lamellar outgrowths of epithelium, which have developed on both anterior and posterior walls of the interbranchial septa. Each gill contains a loop of blood-vessel. There are two very thin layers between the blood and the surrounding water, which thus permit an exchange of gases.

The filaments (sometimes called gill-plates) (Fig. 440) which bound each gill anteriorly and posteriorly, on one side, form a demibranch, and it is the two demibranchs of a septum which then constitute a gill. This means that each cleft is bounded by demibranchs belonging to two gills.

Some forms have external gill-filaments in the very young which are later absorbed.

In sharks that have more than five gill clefts, as well as in the **Cyclostomes**, the first cleft bears gills, but in many elasmobranchs, as well as in the ganoids (sturgeon and

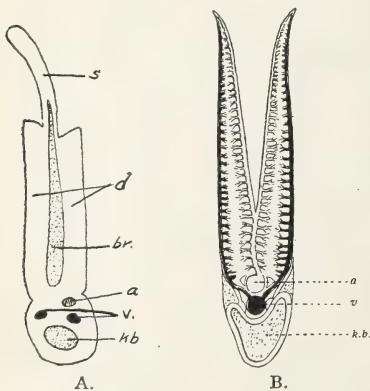


Fig. 440.

Diagram of a gill. *a*, gill-arteries; *br.*, branchial ray; *d*, demibranch; *kb*, cross section of bone of branchial arch; *s*, septum; *v*, veins. (*B*, after Cuvier.)

**Polypterus**), this cleft becomes smaller and smaller until there is only a dorsal opening on the head—the **spiracle**. In most vertebrates this spiracle is closed in the adult, but in the tailless amphibia and the higher mammals the inner portion persists as the Eustachian tube and the greater part of the middle ear.

There are two types of gills in fishes. Practically all the elasmobranchs, with the exception of the **chimaeroids**, have the interbranchial septum well developed so that it extends beyond the demibranchs and thus differentiates an excurrent canal in the cleft. The prolonged septum bends caudally at the outer end to protect the gills from injury.

In teleostomes and chimaeroids the broad fold of the posterior end of the hyoid arch grows backwards over the clefts to form a gill-cover or opercular apparatus. The gill-cover encloses an extrabranchial or atrial chamber into which the clefts empty. The chamber opens by a single slit behind the operculum.

In those instances, just mentioned, where an operculum is developed, the interbranchial septum is always reduced in size until there is only a slender bar from which the demibranchs extend into the atrial chamber. The two opercular folds are usually continuous beneath the pharynx.

In teleosts and ganoids the operculum (gill-cover proper) is usually differentiated from a more ventral portion, known as the **branchiostegal membrane**, which is quite flexible and possesses a skeleton of slender **branchiostegal rays**. The ventral wall of the pharynx in these cases is nothing but a slender bar and is called the **isthmus**.

Just as the air in the lungs in the higher forms of animals is taken in through the outer air passages and then passes through the trachea, bronchia, and bronchioles to the delicate septa in the lungs, so in animals possessing gills there is likewise a delicate septum which separates the blood from the stream of water which is constantly being passed over the gills. Water is as a rule drawn into the mouth and then, as the enlarged oral cavity contracts, it is forced out through the clefts, passing over the gills on its way. In the **Myxinoids** the oesophageo-cutaneous duct probably acts as the incurrent passage when the animal has the front of the head immersed in the flesh of a fish. In the lampreys the water is probably taken and forced out through the gill clefts when the animal is attached to some object. The spiracle serves as an incurrent opening in many elasmobranchs and is provided with a valve which develops from the anterior wall. It closes to prevent any backflow. Sturgeons and **Polypterus** have spiracles throughout life.

Sharks have the gill clefts on each side in the so-called neck region, while skates have them on the lower surface of the body. This difference is brought about by the union of the anterior appendages with the head in skates.

Many teleosts have breathing valves at the mouth-opening which

permit water to enter but not flow out again. In such cases there is a more posterior pair formed by the branchiostegal membrane closing the opercular opening through which the outflow of water may occur.

In some of the teleosts and in such forms as **Polypterus** there is an opercular gill with respiratory functions developed on the inner surface of the operculum while in some of the elasmobranchs (even those in which the spiracle is closed) **pseudobranchs**, composed of vertical folds, are developed on the anterior wall of the cleft. These are homologous with gills, but they are not respiratory as they receive only arterial blood which passes from the pseudobranch to the choroid coat of the eye and sometimes even to the brain.

## AMPHIBIA

In the amphibia, although the gill pouches form just as they do in fishes, the first and fifth never break through, while in nearly all adult forms all the clefts are closed. Exceptions occur in **perennibranchs** and the **derotremes** in which from one to three external openings persist.

In the tailed amphibia and in the caecilians, the operculum is merely a fold of integument in front of the gill-area (Fig. 341). The operculum develops without a skeleton support in the larva of tailless amphibians. This fold grows backward over the gills and fuses. Thus atrial chambers are formed which usually open by a single excurrent pore to the exterior. In a few forms, however, both right and left excurrent openings occur.

It is usually conceded that the gills of amphibia are of ectodermal origin and that both external and internal gills may be present at the same time. In the tailless amphibia, such as frogs, the operculum grows over the gill clefts, and the external gills are folded into the atrial chamber, where they are gradually reduced, while the gills which developed from the walls of the clefts become functional. At the time of metamorphosis, the clefts are entirely closed and the gills absorbed.

It has usually been taught that the gills of fishes are entodermal in origin, but if this is true, they cannot be homologues of the amphibian gills. However, the structures are so much alike in appearance, in structure, and in function, that it seems they must be homologous. Nevertheless, more evidence must be awaited before positive assertions of value can be made.

It may be interesting, and with further knowledge some time it may prove of value to note from the foregoing that amniotes have visceral pouches in the embryo, though gills are never developed in the adult; that reptiles have five of these pouches—birds and mammals four. In man only the first breaks through to form a cleft, while in many of the higher forms there are grooves on the outside of the neck which show their original position. The manner of obliterating these external grooves is as follows: The arches most cephalad, especially the hyoid,

after enlarging, slide back over those lying more caudad so that at least the external branchial grooves lie in a pocket called the **cervical sinus**. This sinus is later closed by a process from the hyoid arch which extends over it quite as in the development of **Anura**. Internally the entodermal branchial pouches, with the exception of the first, disappear, but the first persists as the Eustachian tube and the greater part of the middle ear.

### THE SWIM BLADDER

The swim bladder arises as a diverticulum of the alimentary canal remaining in contact with that canal by a pneumatic duct in the ganoids and one group of teleosts (**Physostomi**) (Fig. 441). This duct, although

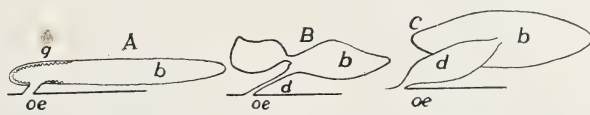


Fig. 441.

Swim-bladders of those fresh-water fish whose air-bladders have a duct (physostomous). *A*, Pickerel; *B*, Carp; *C*, Eel. *b*, swim-bladder; *d*, duct; *g*, red gland; *oe*, oesophagus. (From Kingsley after Tracy.)

usually emptying into the oesophagus, may connect with the stomach. However, in most teleosts the duct disappears entirely at an early date. The swim bladder lies dorsal to the digestive duct outside of the peritoneum, although below the vertebrae and excretory organs. It may be of almost any dimensions, sometimes extending the entire length of the body. In some forms of teleosts, which remain almost constantly at the bottom, it is entirely absent. The swim bladder, although usually unpaired, is paired in most ganoids and may even form three divisions of connecting sacs. There may be diverticula of any and all kinds. The internal part of it may be smooth and simple, or it may be subdivided by various septa, or it may even be alveolar like the lungs of higher vertebrates. There may be striated muscle fibers in the walls. In some **Siluroids** and **Cyprinoids** the walls are even partly calcified because some of the vertebral processes are included in the walls.

The blood supply of the swim bladder is arterial and comes from either the aorta or the coeliac axis; sometimes different portions receive blood from both these vessels. The arteries break up in the walls to become networks of minute vessels known as **retia mirabilia**. These often form "**red spots**" on the inner surface. From the retia the blood passes to the postcardinal, hepatic, or vertebral body-veins in the ganoids and physostomous species, especially in those with a wide pneumatic duct.

The swim bladder contains a greater quantity of  $O_2$  than is found in solution in the water in which the fish lives. It is therefore probably a storage organ for  $O_2$  for use when the fish dives to lake bottoms in

the summer for food. This can be understood the better when it is remembered that there is no  $O_2$  at all at the bottoms of lakes in summer.

The swim bladder is supposed to make it possible for its possessor to regulate its equilibrium while in its watery medium. This supposition has the following facts upon which to rest its validity: ground-feeding teleosts do not have it, but those who must adjust their position in such a way as to obtain the requisite food do have it, while in many of these there is a diverticulum from it to various portions of the ear.

### LUNGS AND AIR DUCTS

In all the higher forms of animals and in some few fishes—dipnoids—the lungs arise as an outpushing from the ventral side of the pharynx immediately behind the last gill pouch. This outpushing divides almost immediately into a right and left half, and just as the outgrowing from the digestive tract carried the covering of that tract before it, so, too, a peritoneal covering is carried before the respiratory organs.

As development goes on, the growing part protrudes into the coelom so that the parts lying therein have an entodermal lining which was derived from the epithelium of the pharynx, while the outer layer of peritoneum is serous mesenchyme carrying blood and lymph vessels as well as nerve and smooth-muscle fibers between the two. That portion of the respiratory system from the pharynx to the lungs consists of trachea, bronchi, and their accessories. These together constitute what are commonly called **air ducts**. The lungs are treated as distinct from these.

On the ventral side of the trachea, in air-breathing animals, there is a separation which forms the **larynx** (Fig. 442), the beginnings of which can be studied in amphibia, in the lower forms of which a simple pair of cartilages are developed on the sides of the **glottis** (the glottis simply being an elongated slit connecting the pharynx with the air ducts). These cartilages develop in the position of a reduced visceral arch. In other forms, such as the **Urodeles**, the more cephalic ends of the lateral cartilages separate from the rest and form an **arytenoid** which is the first of the laryngeal cartilages, and is imbedded in the walls of the glottis. The remaining lateral cartilages may remain as they originally develop or divide into any number of pieces. However, the more cephalic pair of these pieces often fuse in the mid ventral line to form the **cricoid**, which is the second element of the laryngeal framework. Attached to these cartilages there are various **antagonistic muscles** which make it possible to open and close the opening.

The **vocal cords** are formed by a pair of folds of the laryngeal lining, which extend parallel to the margins of the glottis. Sound is produced by the vibrations caused by the air passing over these cords as they are relaxed or tightened in different degrees. The larynx is quite rudimentary in reptiles and birds. In the latter the **syrinx**, shortly to be described, takes the place of the larynx.

In the mammals, one or more **thyroid cartilages** are added on the dorsal side to those already described. In the monotremes, the hyoid apparatus and the larynx are most intimately connected, but in the higher forms of mammals, such an association is not so intimate even in the embryo.

The thyroid cartilage forms a half ring on the ventral side of the anterior end of the larynx in the higher mammals. The anterior dorsal angles form cornua which connect with the hyoid by a ligament. Dorsal

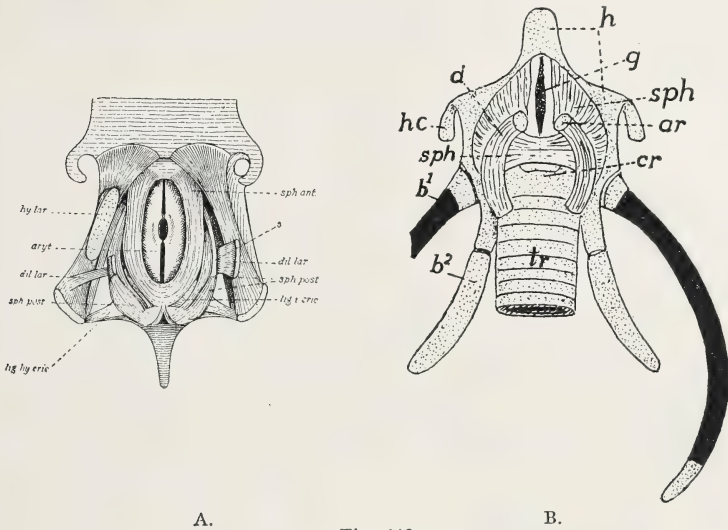


Fig. 442.

*A*, Muscles of larynx (voice box) of *Rana esculenta*. Dorsal view. *aryt.*, arytenoid cartilage; *dil.lar.*, dilator muscle; *hy.lar.*, hyo-laryngeus muscle; *lig.i.cric.*, intercricoideum ligament; *s.*, tendon of posterior sphincter muscle; *sph.ant.*, anterior sphincter muscle; *sph.post.*, posterior sphincter muscle. (After Gaupp.)

*B*, Laryngeal apparatus of a Turtle. *ar*, arytenoid; *b¹,²*, first and second branchial arches; *cr*, cricoid; *d*, dilator laryngis muscle; *g*, glottis; *h*, hyoid; *hc*, hyoid cornua; *sph*, sphincter laryngis; *tr*, trachea. Cartilage is dotted, bone is black. (From Kingsley after Göppert.)

to the thyroid is the **glottis** with the **arytenoids** in its walls. Posterior to the glottis is the ring-shaped **cricoid** which is followed by the **trachea**. Anterior to the glottis lies the epiglottis which is a fold of mucous membrane supported by an internal cartilage which articulates with the anterior margin of the thyroid. The epiglottis usually stands erect, thus leaving the glottis open during respiration, while during deglutition it is pulled back into the glottis, supposedly preventing the entrance of food into the trachea, but there are numerous cases on record where the epiglottis has been removed and such individuals seem to have no difficulty with their food getting into the "wrong throat."

The cavity of the larynx bears a **vocal cord** internally on either side. These are folds of the mucous membrane which extend from the thyroid to the arytenoids. By moving these latter cartilages they can be

tightened or relaxed to alter the pitch of the note caused by their vibration. A pocket lies anterior to the cords, the **laryngeal ventricle (sinus of Morgagni)**, one on each side, quite small in most mammals but well developed in the anthropoid apes to large vocal sacs. In the chimpanzee there is a median vocal sac in addition. These act as resonators and add strength to the voice.

The larynx is prolonged in whales and marsupials so that it projects into the choana behind the soft palate. This is an adaptation to the manner of taking food from the water and breathing at the same time in the whales. In young marsupials the milk is forced into the mouth by the muscles of the mammae of the mother; an arrangement that prevents strangulation.

The trachea (Fig. 442) in the higher forms has a **series of cartilaginous rings** forming its walls. It varies in length and size as well as in the quantity of cartilage which strengthens its walls in the different genera. It is, as a rule, shortest in lizards and often convoluted in turtles. The cartilaginous rings may be entirely complete or the dorsal part of the ring may be of membrane. It is usually longest in birds.

It is interesting to note that the larynx never forms the voice organs of birds. In this form of animal life, the sound producing parts are formed from membranes which also vibrate by the passage of air but the voice organ is located at the point where the trachea divides into bronchi and is known as a **syrinx** (Fig. 443). The most common form of this organ is that in which the last rings of the trachea unite to form

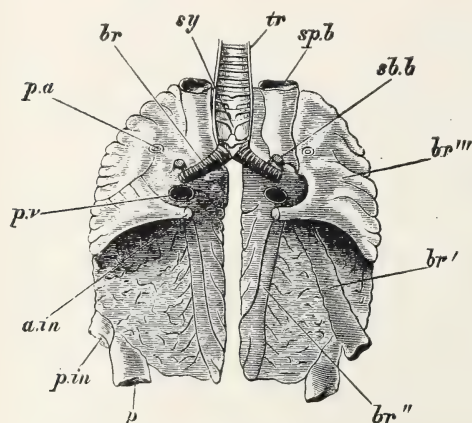


Fig. 443.

*Columba livia*. The lungs with the posterior end of the trachea, ventral aspect. *a.in.*, aperture of anterior thoracic air-sac; *br.*, principal bronchus; *br'*, *br''*, *br'''*, secondary bronchi; *p.*, aperture of abdominal air-sac; *p.a.*, pulmonary artery entering lung; *p.in.*, aperture of posterior thoracic air-sac; *p.v.*, pulmonary vein leaving lung; *s.b.b.*, aperture of interclavicular air-sac; *sp.b.*, aperture of cervical air-sac; *sy.*, syrinx; *tr.*, trachea. (From Parker's *Zootomy*.)

a **resonating chamber**, the **tympanum**, while folds of membrane, called internal and external tympanic membranes (not to be confused with the similarly named structure in the ear), extend into the cavity from the median and lateral wall of each bronchus.

In some instances there is also an internal skeletal element, called a **pessulus**, bearing a semilunar membrane on its lower surface. This type of syrinx may be symmetrical and may even form a bony resonating vesicle. There are various muscles attached to trachea and bronchi, which permit an alteration of the tension of the folds in all forms of

the syrinx so as to make possible a change in the sounds uttered.

In mammals the cartilaginous rings of the trachea are dorsally incomplete; this position being closed by membrane. A structure of this kind permits the tube to remain open and yet also permits it to "give" a little when food passes down behind it through the oesophagus.

## THE LUNGS

In the lung fishes there is usually a single sac, although several types of these animals have **paired lungs**. The pulmonary arteries spring from the **last efferent branchial artery** of both sides. The blood supply, therefore, under normal conditions is arterial, and the lungs cannot act as respiratory organs. In times of drought (**Protopterus**), or when the water is fouled (**Ceratodus**), the gills no longer function, and the pulmonary arteries bring venous blood to the lungs.

In amphibia the two lungs are elongated. They are united at their bases though true bronchi are absent. They may or may not have alveoli. In the frog the two lungs are distinct, the walls being divided into a series of sacs or infundibula lined with alveoli. The infundibula open into a central chamber, which, since it is ciliated and has numerous glands in its walls, may be compared to a bronchiole.

In those terrestrial urodeles which are lungless in all stages of development, no traces of larynx or trachea occur at all, even after the gills are absorbed. In such species there is a considerable development of capillaries in the skin as well as in the walls of the mouth and pharynx, so that the respiratory functions are transferred to these parts. In the frog, as already shown, the skin is respiratory and largely supplied by the cutaneous arteries arising from the same arch as the pulmonary arteries.

The air ducts enter the anterior end of the lungs in amphibia, while in higher forms the lungs extend anteriorly to the entrance of the bronchi on the medial side. This change is in part the result of the transfer of the heart into the thorax, due to the position of the pulmonary arteries which force the bronchi toward the center of the lungs. In amniotes, also, the ducts are characterized by the presence of cartilage in their walls, so that they are true bronchi. The bronchi may extend inside of the lungs and divide into secondary and tertiary bronchi.

The lungs of reptiles are often non-symmetrical; sometimes one is even absent. In the snakes the lungs consist of a single sac lined with infundibula either in part or throughout. In the lizards there are one or more verticle septa dividing the lung into chambers lined with alveoli while a part of the bronchus may extend to the extremity of the lungs. The septa in the chameleons do not reach the distal wall; consequently, the chambers communicate so that the bronchus enters a cavity known as the **atrium**. This connects with the various chambers separated by the septa and these in turn open into a terminal vesicle. This whole

structure seems to anticipate the **parabronchi**—the small uniform sized air-tubes in the lungs of birds, which connect the larger secondary branches of the bronchial tubes. This resemblance is increased by the development in these same lizards of long, thin-walled sacs from the posterior part of the lungs, which extend among the viscera, even into the pelvic region. The air sacs are used to inflate the body. It is well to remember and apply what has just been said to the study of similarly named structures in the bird. In turtles and crocodiles there is no atrium and the whole lung has a spongy texture. The bronchus in turtles enters on the ventral side of the lung and not as in lizards in the medial.

## SUMMARY OF THE RESPIRATORY SYSTEM BALANOGLOSSUS

The pharyngeal clefts take the form of gill sacs, each of which opens into the pharynx in a U-shaped slit, resembling that of **Amphioxus**, and opens to the exterior by a small pore. These gill-slit openings to the pharynx are supported by thin, chitinous bars resembling the gill bar system of **Amphioxus**.

## FISHES

The characteristic respiratory organs of aquatic vertebrates are **gills** or **branchiae**. Gills are finely divided comb-like outgrowths of the ectodermal or endodermal epithelium lining the branchial clefts. The number of clefts or gill slits vary from five to seven in number. Each cleft is separated from its neighbor by branchial septa. The more primitive the fish, the larger number of branchial clefts it is likely to have. The modern types have regularly five clefts. **Heptanchus**, sometimes mentioned as the most primitive living species of shark, has seven clefts, while **Hexanchus**, another primitive shark, has six, and elasmobranchs in general have five fully developed clefts and a vestigial anterior first cleft called a **spiracle**.

The spiracle is the rudimentary first cleft, which is also found among the most primitive teleostomi (**Crossopterygii** and **Chondrostei**). It is present in the embryos of **Teleostei** and **Holocephali**, although here it is closed before hatching. In the **Holocephali**, an aberrant group of elasmobranch fishes, the fifth cleft is closed in the adult, which reduces the number of functional clefts to four. The cyclostomes have on the whole a larger number of clefts than the true fishes. However, the hag-fishes (Fig. 366) of the family **Myxinidae** have no more than six pairs, while those of the family **Bdellostomidae** (Fig. 366) have as many as fourteen pairs, and the lampreys all have seven pairs.

The direction of change in fishes appears to be one of reduction in the number of clefts from fifty or more in **Amphioxus** (Fig. 437) and **Ascidians** (Fig. 313), to fourteen to six in the cyclostomes, seven to five in the true fishes, and four in the **Holocephali**.

The openings of the clefts to the exterior differ in different groups of fishes. Among the elasmobranchs each cleft usually opens separately and is not covered by any flap or operculum, although in **Chlamidoste-lachus**, the primitive frilled shark, each cleft has a backwardly directed flap or gill cover. The first three clefts in the **Holocephali** are covered by an operculum, and only the fourth, or the last functional, cleft opens freely to the outside. In the great majority of teleostomi and in the **Dipneusti**, the five clefts are covered with a flap-like operculum, capable of opening and closing, thus effectively protecting the branchial filaments from injury. In some of the eels and in other specialized teleosts, the gills are completely covered with a fold of skin, the only exit being through one or two small water pores. There are two quite different and distinct kinds of gills found among fishes, namely: **external** and **internal gills**.

External gills are purely larval or embryonic organs. They are not functional in any adult fish. Their homologues are found in the perenni-branchiate amphibia and are believed to be **paedogenetic** or **permanent larval types**. External gills are finely branched processes of the ectodermal epithelium of the branchial tract. They are found in the embryos of many elasmobranchs and in some teleosts. A notable case of larval gills is seen in the advanced larva of **Polypterus** (Fig. 368).

The true functional gills of adult fishes are internal. They are finely divided diverticula of the endodermal epithelium of the branchial clefts. The nasal cavities are blind sacs which do not communicate with the mouth. Such communication begins with amphibia.

## THE AIR-BLADDER AND ACCESSORY ORGANS OF RESPIRATION

In all of the groups of fishes above the elasmobranchs there is a single, or paired, **air-bladder** (probably homologous with the lungs of higher forms), a sac-like diverticulum of the pharynx, derived from either dorsal or ventral sides of the alimentary tract. It is in all cases supplied with blood from the pulmonary artery (which, in turn, arises from the last efferent artery of either side), and, primitively at least, subserves two functions: (1) that of a hydrostatic or buoyancy organ, and (2) that of an accessory respiratory organ or primitive lung. In the most primitive teleostome fishes, the **Crossopterygii**, it is used as a lung when the water is foul; in **Amia**, it is constantly functional as an air-breathing apparatus; while in the **Dipneusti** (lung-fishes), it is an elaborately pouched lung used to tide the fish over a period of drought.

In certain other fishes that have acquired terrestrial habits, such as the climbing perch, **Anabas** (Fig. 371), which will drown if immersed in water, and the air-breathing eel, **Clarias**, there is an extensive post-branchial chamber, provided with labyrinthine, or arborescent, elabora-

tions of the epithelium that are highly vascular and play a pulmonary role.

### DOGFISH

Here branchial respiration is carried on in the six pairs of branchial clefts. These branchi are primitive respiratory organs, consisting of mere diverticula of mucus membrane, richly vascular, and supported by cartilaginous processes called gill-rays. The water enters the mouth and is forced out through the gill slits. In doing so it aerates the gill filaments, and provides oxygen for the blood which circulates rapidly through them.

### AMPHIBIA

External gills are found in the perennibranchiate urodeles (Fig. 374) throughout life and in practically all amphibians while in the larval stage.

The epithelium covering these external gills is ectodermal so that they are really cutaneous and not pharyngeal gills. They are, therefore, of a totally different nature from the so-called external gills of the embryos of **Elasmobranchs** and **Holocephali**, in which case the external gills are only filaments of the internal gills prolonged through the branchial openings.

Internal gills develop only in the larvae of **Anura** and are probably homologous with the internal gills of fishes although even here the epithelium may be ectodermal. In many species of Salamanders, lungs are absent, but in most amphibians, they develop as ventral outgrowths from the oesophagus. The left is usually the longer. The lungs are united at their base, although true bronchi are absent. In the lungless Salamanders respiration is exclusively cutaneous and pharyngeal. The lungs are supposed to have secondarily disappeared in these animals. The air ducts enter the anterior end of the lungs in amphibia, while in amniotes the lungs extend cephalad to the entrance of the bronchi which is on the medial side. This change is due to the transfer of the heart into the thorax so that the pulmonary arteries then force the bronchi toward the center of the lungs. The ducts in the amniotes have cartilage in their walls; they are thus true bronchi. These bronchi often extend into the lungs where they divide into secondary and tertiary bronchi.

### REPTILIA

Gills are absent and gill-slits disappear in all animals higher than Urodeles. The lungs are large and complicated and often non-symmetrical; sometimes one is lacking. In the snakes, the lungs consist of a single sac lined with infundibula either in part or throughout. In the lizards there are one or more vertical septa dividing the lung into chambers lined with alveoli, while a part of the bronchus may extend

to the extremity of the lungs. In the chameleons, the septa do not reach the distal wall; consequently, the chambers communicate so that the bronchus enters a cavity known as the **atrium**. This connects with the various chambers separated by the septa, and these in turn open into a **terminal vesicle**. This whole structure seems to anticipate the **parabronchi**—the small uniform sized air-tubes in the lungs of birds—which connect the larger secondary branches of the bronchial tubes. There develop in these lizards long, thin-walled air-sacs from the caudal portion of the lung. These extend among the viscera even into the pelvic region. The air sacs are used to inflate the body. In turtles and crocodiles there is no atrium, and the whole lung has a spongy texture. The bronchus in turtles enters on the ventral side of the lung and not as in lizards on the medial.

Inhalation and exhalation are effected partly by drawing in the neck and thrusting it out again so as to decrease and increase the volume of the thoracic cavity. The air is also swallowed into the lungs by filling and then emptying the throat.

## BIRDS

Birds have large lungs each of which possesses nine small air-sacs. The air enters the bronchi and passes to the air-sacs. The air is thus warmed before being taken into the alveoli of the lungs. It makes its exit through the excurrent bronchi. A complete change of air occurs at each inspiration and expiration. The trachea and the larger bronchi are kept open by means of rings of cartilage; the trachea is enlarged, just before it divides, into a **syrix** or voice box (Fig. 443), a structure limited to birds, in no way homologous with the larynx of mammals. The mechanics of voice production in birds depends upon forcing the air through a flexible valve which is set into vibration. The lungs also connect with visceral air-sacs and with **air-spaces** in the **bones**.

## MAMMALS

There are two points of view regarding the relation of mammalian lungs to the respiratory apparatus of the lower forms of animals. One view holds that the lungs are merely a further development of the air-bladder of fishes; the other insists that they are more likely to be modified gill-pouches which have grown caudally into the coelom instead of opening to the exterior by growing laterally.

The fact, however, that the pneumatic duct is dorsal in position and the blood supply is arterial makes the first view seem improbable. The latter view is supported by the fact that the lungs are paired outgrowths from the pharynx immediately caudal to the last gill clefts and in serial order with them. The blood supply from the sixth arterial arch would be in full accord with this view. Then, too, both in the earlier stages

and in the primitive forms, the skeletal support of larynx and trachea has the relations and appearance of rudimentary gill-arches, while the muscles surrounding this region are modified from those of the visceral arches.

Each lung is enclosed by a pleural membrane and the pleural cavity, in which it lies, is cut off entirely from the rest of the coelom by the muscular diaphragm. This muscle usually lies transverse to the main axis of the body. It is attached close to the inner margin of the lower ribs and extends headward as a sort of tent or dome. The lungs may be divided into lobes and lobules. The right one usually has the greater number. In whales, elephants, and odd-toed ungulates there may be no lobules at all. In the monotremes only the right lung has lobes.

From the main bronchial tube there are dorsal and ventral secondary bronchi; the ventral redivide. When the more cephalic bronchi lie in front of, or above, the pulmonary artery, they are called **eparterial bronchi** while the others are known as **hyparterial**.

Respiration is made up of inspiration and expiration. This has already been described in the study of the frog. Little is known regarding this process in turtles and other reptiles. In birds, the lungs are definitely attached to the ribs and vertebrae so that with every motion there is both a change in shape and size.

In the mammals, the ribs lie at an oblique angle to the vertebral column. As the intercostal muscles are contracted and relaxed, the ribs turn slightly and can increase and diminish the size of the thoracic cavity.

The diaphragm forms a complete partition between the thoracic and abdominal cavities and aids materially in respiration as it flattens when contracted. This increases the size of the pleural cavity and draws in air through the trachea. The abdominal muscles likewise play a part. Expiration is caused in part by the action of the intercostal and abdominal muscles and in part by the elastic tissue and smooth muscles in the lungs themselves.

### ACCESSORY RESPIRATORY APPARATUS

It will be recalled that the entire respiratory tract grows from the primitive digestive tract. It is, therefore, not difficult to understand that there are certain fishes which use a caudal portion of the digestive tract for respiration. In **Cobitis**, water is drawn in and expelled through the anal opening. The more caudal end of the digestive canal is very vascular and is used in respiration.

Among the amniotes, the lungs are not functional either before hatching or before birth. Still, oxygen is necessary for the development of the embryo and the carbon dioxide which has formed must have an

outlet. The organ used for this combined respiratory and excretory function is called the **allantois** (Fig. 363). This is the ventral diverticulum from the more caudal part of the digestive canal which has already been studied in our work on Embryology. It becomes larger with the growing embryo. It is extremely vascular and is absorbed in some forms such as the Sauropsida or is drawn off with the placenta in mammals. The basal part, however, persists as the urinary bladder.

## CHAPTER XXV

### THE CIRCULATORY SYSTEM

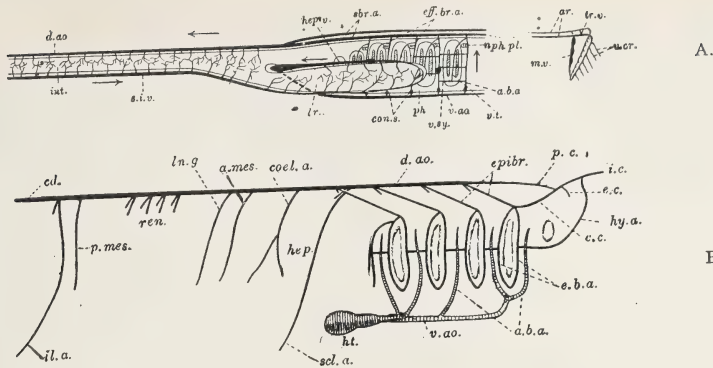
**T**O understand the modern interpretation of the circulatory system, it is necessary to have clearly in mind what is called the probable ancestral condition of this system in the lower forms of animals. Thus one may observe how in each of the succeeding higher forms something is added to the development of the animal of the next succeeding scale below.

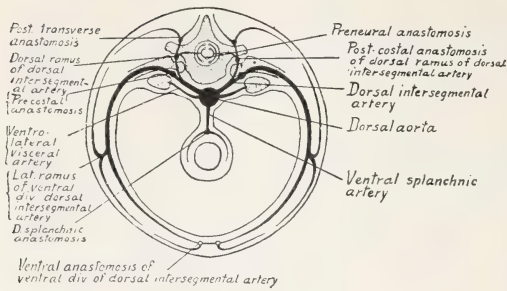
Some have thought that the original circulation consisted of a lymphoidal liquid alone and, then, as time went by, this type of circulation specialized into what we now term a blood circulation. It is thus supposed that the lymph vessels, as we find them in modern forms of living animals, furnish a clue as to how the primitive systems of vessels appeared. It is all quite speculative, however. Another explanation, which has more plausibility in its favor, is that the main blood vessels are the remnants of the segmentation cavity which have become obliterated by the growth of mesoderm; the part not obliterated then became the blood vessels.

In any explanation that is built upon the Haeckelian "law" of biogenesis there not only remains much to be explained but various occurrences even must **be explained away**. In this theory, it is supposed that much of the race history has been lost in development, while a development of additional vessels of various kinds has covered up some of the older developmental processes.

Many blood vessels, which should arise as fissures between other tissues, are found to be formed as solid cords of cells. These may later form a lumen and be converted into tubes; in other instances vessels which originate separately in the embryo may fuse together during development to form a single one.

There are various main points, however, which must be understood in any discussion of the blood system (Fig. 444, A, B). There is a dorsal tube carrying the blood toward the tail. From this tube various vessels extend toward the right and left at almost right angles through the dorsal tube. Those that pass toward the outer side of the animal are called **somatic**, while those that pass toward the inner region are called **splanchnic** vessels. These transverse vessels connect with two ventral, longitudinal tubes, one of which is in the wall of the digestive tract which runs headward and unites with the other one which has passed through the ventral body wall, so that, after the union of the two, a single tube is found coursing to the head end of the body. In one of the lowest forms of chordates, namely, the **Amphioxus**, various parts of this system develop muscle walls and then act as pumping organs.





H.

Fig. 444.

Comparisons of Circulatory systems. *A*, a diagram of the vascular system of *Amphioxus*, from the right side. *a.b.a.*, Afferent branchial arteries; *ar.*, carotid continuations of the suprabranchial arteries; *cons.s.*, contractile swellings on the afferent branchial arteries; *d.ao.*, dorsal aorta; *eff.br.a.*, efferent branchial arteries; *hep.v.*, hepatic vein; *int.*, intestine; *lr.*, liver; *m.v.*, "moniliform" vessel from left carotid; *nph.pl.*, nephridial plexus; *ph.*, pharynx; *s.i.v.*, subintestinal vein; *sbr.a.*, suprabranchial arteries; *tr.v.*, transverse vessel joining the carotids; *v.ao.*, ventral aorta; *v.cr.*, vessels of cirri; *v.sy.*, vessels of synapticulæ; *v.t.b.*, vessels of tongue-bars.

*B*, A diagram of the arterial system of a dogfish, seen from the right side. *a.b.a.*, Afferent branchial arteries; *a.mes.*, anterior mesenteric artery; *c.c.*, common carotid artery; *cd.*, caudal artery; *coel.a.*, coeliac artery; *d.ao.*, dorsal aorta; *e.b.a.*, efferent branchial arteries; *e.c.*, external carotid artery; *epibr.*, epibranchial arteries; *ht.*, heart; *hep.*, hepatic artery; *hy.a.*, hyoidean artery; (this joins the internal carotid of the opposite side, which is not shown); *i.c.*, internal carotid artery; *il.a.*, iliac artery; *ln.g.*, lienogastric artery; *p.c.*, posterior carotid artery; *p.mes.*, posterior mesenteric artery; *ren.*, renal arteries; *scl.a.*, subclavian artery; *v.ao.*, ventral aorta. (From Borradaile.)

*C* and *D*, Comparison of the venous systems of the dogfish and a teleost. *anas.*, anastomosis between the two posterior cardinals; *ao.v.*, ventral aorta; *atr.*, atrium; *brach.*, brachial vein; *card.ant.* and *card.post.*, anterior and posterior cardinals; *caud.*, caudal vein; *cl.*, cloacal vein; *con.art.*, conus arteriosus; *duct.cuv.*, duct of Cuvier; *hep.*, hepatic vein; *hy.*, hyoid vein; *il.*, iliac vein; *jug.inf.*, inferior jugular vein; *lat.*, lateral vein; *leb.*, liver; *mand.*, mandibular vein; *n.*, kidney; *port.*, hepatic portal vein; *port.ren.*, renal portal vein; *segm.*, segmental veins; *s.int.*, subintestinal vein; *sin.hy.*, hyoid sinus; into which the veins from the mandibular and hyoid arches open; *sin.orb.*, orbital sinus; *sin.ven.*, sinus venosus; *sperm.*, spermatic vein; *subsc.*, subscapularis vein; *subcl.*, subclavian vein; *schw.bl.*, veins of the swim-bladder; *ventr.*, ventricle. (Both figures from Boulenger, A after Parker.)

*E*, A diagram of the venous system of the dogfish. *a.c.s.*, Anterior cardinal sinus; *c.v.*, caudal vein; *d.C.*, ductus Cuvieri; *h.p.v.*, hepatic portal vein; *h.s.*, hepatic sinus; *hy.s.*, hyoidean sinus; *i.j.s.*, inferior jugular sinus; *i.o.s.*, interorbital sinus; *il.s.*, iliac sinus; *int.*, intestine; *k.*, kidney; *lat.s.*, lateral sinus; *lr.*, liver; *n.s.*, nasal sinus; *or.s.*, orbital sinus; *p.c.s.*, posterior cardinal sinus; *r.p.v.*, renal portal vein; *s.v.*, sinus venosus; *scl.s.*, subclavian sinus. (From Borradaile.)

*F*, A diagram of the principal arteries and veins of a pigeon. *ao.*, Aortic arch; *Br.a.*, brachial artery; *Br.v.*, brachial vein; *C.*, carotid artery; *c.m.*, coccygeo-mesenteric vein; *d.a.*, dorsal aorta; *F.*, femoral vein adjoining femoral artery; *h.v.*, hepatic veins; *il.*, internal iliac artery and vein; *i.v.c.*, inferior vena cava; *j.*, jugular vein; *l.a.*, left auricle; *P.*, right pulmonary artery; *P.c.a.*, pectoral artery; *P.c.v.*, pectoral vein; *ra.*, right auricle; *rp.*, hypogastric vein; *rv.*, renal vein; *sc.*, sciatic artery and vein. Near the apex of the ventricle the coeliac and anterior mesenteric arteries and the epigastric vein are shown, but not lettered. At the hinder end of the figure the caudal and posterior mesenteric vessels are shown, but not lettered.

*G*, The circulatory system of the rabbit. (a) Letters to right—*e.c.*, External carotid; *i.c.*, internal carotid; *e.j.*, external jugular; *scl.a.*, subclavian artery; *scl.v.*, subclavian vein; *p.a.*, pulmonary artery (cut short); *p.v.*, pulmonary vein; *L.A.*, left auricle; *L.V.*, left ventricle; *d.ao.*, dorsal aorta; *h.v.*, hepatic veins; *c.*, coeliac artery; *a.m.*, anterior mesenteric; *s.r.b.*, suprarenal body; *l.r.a.*, left renal artery; *l.r.v.*, left renal vein; *K.*, kidney; *p.m.*, posterior mesenteric artery (incorrectly shown as if paired); *spm.*, spermatic arteries and veins; *c.i.a.*, common iliac artery. (b) Letters to left—*p.f.* and *a.f.*, posterior and anterior facial; *e.j.*, external jugular vein; *i.j.*, internal jugular; *R.Scl.*, right subclavian artery; *S.V.C.*, superior vena cava; *R.A.*, right auricle; *R.V.*, right ventricle; *I.V.C.*, inferior vena cava; *r.r.a.*, right renal artery; *r.r.v.*, right renal vein; *s.r.b.*, suprarenal body; *spm.*, spermatic arteries and veins; *il.*, ilio-lumbar vein; *f.v.*, femoral or external iliac vein; *i.il.v.*, internal iliac veins. (From Thomson.)

*H*, Diagram of intercostal (intersegmental) arteries.

In all vertebrates the heart lies on the ventral side of the digestive tract covered by a pericardial sac. This sac is really a part of the coelomic lining. The various large blood vessels, carrying blood from the heart to the general system, are known as **aortae** and the large veins returning the blood directly into the heart are usually called **venae cavae**.

The ventral aorta gives off various pairs of vessels called the **aortic arches** which are situated on each side of the pharynx in the grooves called the **gill septa**. These arches run from the ventral aorta around the digestive canal to the dorsal side where they unite to form a longitudinal canal. That is, the arches along each side form a separate canal at first; then the two canals unite to form the **dorsal aorta**, which runs caudad the entire length of the body. There may be, and usually are, various small arteries arising from any or all of these arterial arches. It is necessary that the student know **what becomes of the aortic arches** and in what groups of animals certain ones disappear and others remain functional. The **first pair** of arches lying toward the head end give rise to both the **internal carotid artery** which goes to the brain, and the **external carotid** supplying the more superficial portion of the head. The arteries which arise from the dorsal aorta are either **somatic or splanchnic**, that is, either supply outer or internal portions of the body. Examples of somatic blood vessels are the **intercostal** (intersegmental) **arteries** running between the ribs. The **mesenteric arteries**, which are distributed primarily to the alimentary canal, are of the splanchnic type.

The **subclavian artery**, which supplies the arms of the animal, and the **iliac artery**, which supplies the hind limbs, are some of the larger and more common of the somatic arteries.

The splanchnic or visceral arteries do not show much trace of segmentation. They are distributed to the walls of the digestive tract. Two pairs, however, of these vessels are of special importance, namely, a pair of **omphalomesenteric arteries** in front and a pair of **hypogastric arteries** (internal iliac) near the origin of the iliac arteries (Fig. 450).

There are really no **end arteries** or veins. All arteries carry blood to certain parts of the body through minute capillaries which then anastomose with the venous capillaries which drain the various parts the arteries supply.

The head is drained by a pair of **jugular veins** easily seen above the mouth. In fishes there is also a pair of **inferior jugulars** in the region of the lower jaw and the lower side of the gill arches. These veins run caudad to the level of the **sinus venosus** where they are joined by a **post-cardinal** coming from the excretory organs. The jugular and post-cardinal on each side unite to form a trunk which runs transversely and empties into the sinus venosus. This is called the **Cuvierian duct**. A pair of **omphalomesenteric veins** enter the sinus venosus from the caudal side. These are continuations of a **subintestinal vein** running

alongside the liver after having passed along the ventral side of the digestive tract. This subintestinal vein forms a loop around the anal opening and extends to the end of the tail as the **caudal vein**. The **subclavian vein** from the arm may empty either into the jugulars or the post-cardinal near the Cuvierian duct. The blood from the hind limb leaves by an **iliac vein** on each side and runs forward on the lateral body wall. It is called the **lateral abdominal vein**. This also enters the Cuvierian duct.

Omphalomesenteric and subintestinal veins belong to the visceral or splanchnic group. The others are somatic. The vessels mentioned are important and should be known thoroughly because they develop very early in the embryo, and, practically all later developments as well as modifications that take place in them, can only be discussed intelligently when the basic structures just mentioned are known. There is probably no more variable system in the body (even in the same species) than the vascular.

## DETAILED STUDIES

### THE HEART

The heart itself is a **muscle** with a distinctive cellular structure. This cellular structure is a sort of "cross" between voluntary and involuntary muscle. The muscle fibers are striated but run in a **syncitial form** (Fig. 23, Vol. I). The muscular walls of the heart itself are known as **myocardium**. The inner layer of the heart, corresponding to the endothelium of the blood vessels and continuous with them, is called **endocardium**, while the covering of the heart is known as the **pericardium**. Lying between the myocardium and the pericardium is a serous liquid called **pericardial fluid**.

We have already discussed a part of the embryonic method of heart development, but it is necessary here to enter into more detail. The lateral plates of the walls of the coelom grow centrally beneath the digestive canal. There are four regions discernible in these lateral plates, namely: the splanchnic or visceral, the mesenterial and somatic walls, and the coelomic cavity.

Between the coelomic walls and the endoderm, one may observe various cells called **vascular cells**. It is supposed that they find their origin from the mesothelium. Those that lie most dorsalward assist in forming the dorsal blood vessels while those lying ventrad contribute to the heart and the ventral trunks. The two lateral plates just mentioned continue until they meet in a ventrad region. This forms the **ventral mesocardium** (Fig. 344). A little later the dorsal region comes together to form the **dorsal mesocardium** so, that now, that which was formerly a groove has become a **definite tube**. The ventral fusion has disappeared so as to leave the dorsal part attached; this causes the two coelomic cavities to unite and form the **pericardial cavity**.

In turtles and crocodiles there is a small portion of this ventral mesocardium remaining, which connects the apex of the heart to the pericardial wall. The walls of this tube are now called the **myoepicardial mantle**, and the vascular cells enclosed within this mantle form a continuous sheet and become the endocardium or lining of the heart.

There are still some vascular cells cephalad and caudad to this tubular heart. These furnish a lining for the blood vessels which arise from the edges of the lateral plates and connect with the heart. The first vessels toward the head end (the **anterior pair**) become the **mandibular arteries**, while those lying caudad to the heart (the posterior) are called the **omphalo-mesenteric veins**.

It is at this time also that immediately cephalad to the omphalo-mesenteric vein a transverse tube appears on each side connecting with the heart tube. These tubes are the ducts of Cuvier. The ridge, where the Cuvierian ducts grow, becomes larger until it forms a transverse partition known as the **septum transversum** (Fig. 348). It is this septum, or partition, which separates the heart cavity or pericardial region from the abdominal or peritoneal cavity. In the myxinoids and elasmobranchs this septum never completely closes dorsally but leaves one or two openings known as the **pericardio-peritoneal canal**.

Where the early embryo is closely appressed to the very large yolk sac, as in the bony fishes and in all amniotes, the development of the heart is modified. The pharynx is not complete below at first but communicates ventrally with the yolk. The two hypomeres are thus prevented, for a time, from meeting ventrally. Each hypomere, however, is accompanied by its vascular cells. Its edge becomes grooved while the grooves are rolled into a pair of tubes lined with endocardium. The anlage of the heart consists of two vessels (Fig. 283) for a time, each connected in front and behind with its own mandibular artery and omphalo-mesenteric vein and surrounded with its pericardial sac. Later the two tubes approach and fuse. The formation of mesocardia taking place as before, the mesocardia soon disappear and the whole appears much as in the small-yolked forms.

The pericardium is relatively large at first, but in adult forms it is usually quite close fitting to the heart when the heart is expanded.

It must not be forgotten that in **systole** the heart contracts and becomes considerably smaller than normal and that in **diastole** it expands and attains its full size, filling the pericardium accordingly.

It can readily be understood that, so long as the mesocardia are present, the heart tube will be a straight canal connected with the pericardial sac in front and behind. However, as the mesocardia entirely disappear in due time and the heart tube continues to grow, it bends upon itself, something like a capital letter "S," the bending or flexure being largely in a vertical plane (Fig. 283).

At the middle point of the bend the tube remains quite small and here is formed what is called the **atrio-ventricular canal** (Fig. 445). It is in front and behind of this canal that the walls become thickened and the lumen enlarged. The caudal end, which is also the dorsal in this case, forms the chambers known as the **atrium** or **auricle**; the ventral end becomes the **ventricle**. Caudad in the atrium there is a constriction forming a second chamber called the **sinus venosus**. It is into this chamber that the Cuvierian ducts and the omphalo-mesenteric veins enter. The ventral parts of the heart-tubes also form a smaller trunk, called the **truncus arteriosus**, while the **ventral aorta** connects this portion of the heart with the **mandibular arteries** already mentioned.

While the heart is really a muscle, or rather many interwound bundles of muscles, there are certain parts, such as the **sinus venosus**, in which the muscle cells themselves are somewhat scanty as compared with other parts of the heart.

The endocardium develops folds, or **valves** (Fig. 445), in certain places so that blood may flow forward but not backward, and this valvular part of the truncus is known as the **conus arteriosus**. In the vertebrates, this conus is reduced to a single row of valves with the exception of the elasmobranchs, ganoids, and amphibia. The valves lie between the auricle and the ventricle and are prevented from being pushed up into

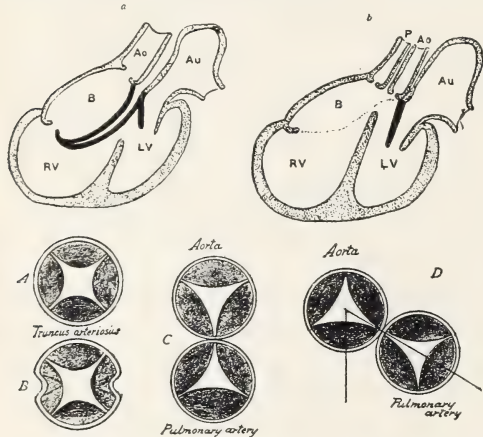


Fig. 445.

*a* and *b*, Reduction of the bulbo-ventricular fold of the heart. *Ao*, aortic bulb; *Au*, atrium; *B*, bulbus cordis; *RV*, right ventricle; *LV*, left ventricle; *P* (in *b*) pulmonary artery. (After Keith.)

*A*, *B*, *C*, *D*, Scheme showing division of bulbus cordis and its thickenings into aorta and pulmonary artery with their valves. The division begins in *B*, the lateral thickenings dividing respectively into *a*, *e*, and *c.f.* Rotation from right to left shown in *D*. (After Heisler.)

the auricle (when the heart contracts and immense pressure is brought to bear upon them) by little ligaments, called **chordae tendineae**, which extend from the edges of the valve to the opposite wall of the ventricle. They are kept taut during systole by capillary muscles, called **columnae carneae**. There is also a valve between the auricle and the sinus in some vertebrates where the hepatic vein enters into the sinus.

If the conus arteriosus is followed by a strong muscular region this is called the **bulbus arteriosus**. The bulbus is composed of regular heart muscle while the truncus is composed of muscles like the rest of the blood vessels. It is for this reason that both conus and bulbus are regarded as a part of the heart while anything cephalad to these is considered a part of the ventral aorta.

## THE VASCULAR SYSTEM

After food has been taken into the digestive tract and digested and the little villi of the small intestines have absorbed the semi-liquid food, this newly absorbed food is ready to become a part of the blood. An elaborate system of blood vessels with a wonderfully intricate and elaborate pumping apparatus—the heart—carries this nourishment to every part of the body.

Before taking up the development of this system, known variously as the **circulatory**, or **vascular**, system, it is necessary that the student understand quite thoroughly what the adult organs are like and what their function is. Only then may one validly attempt to ascertain how and why the organs are placed where they are and how and why their function is what it is. The central part of the vascular system is the heart. In the mammal, this consists of four definite chambers—**two auricles** at the broad end of the heart, and **two ventricles** toward the lower or apex region. The structure of the heart itself is muscular. The compartments of the heart and the work they do belong to the circulatory system proper and will be described here.

Every blood vessel **leaving the heart**, no matter whether it carries arterial or venous blood, is called an **artery**, and every blood vessel **entering the heart** is called a **vein**. This distinction must be kept very clear.

Then, too, it must never be forgotten that blood entering the heart through a vein **always enters a sinus or auricle**. This auricle acts as a reception-chamber for all blood entering the organ. After the blood has entered this chamber, it passes downward through an opening into one of the ventricles, and it is **from the ventricle** that the blood leaves the heart.

In the higher forms of mammals, such as man (Fig. 445), blood enters the right auricle through the large **venae cavae**, and then passes downward through the **auricular-ventricular** opening into the right ventricle. From here it passes through the **pulmonary artery** to the lungs to be **aerated** (that is, to be thoroughly mixed with oxygen and to lose the carbon dioxide that it has gathered in draining the entire body). After being aerated, the blood passes back to the left side of the heart through the **pulmonary vein** to enter the left auricle, and then passes down through a **left auricular-ventricular opening** into the ventricle. From the ventricle the blood stream is sent forth through the **aorta** to all parts of the body, supplying the parts with food and nourishment.

The system just described is known as the **systemic** because the blood which leaves the heart **through the aorta** nourishes all parts of the body.

The arteries break up into smaller **arterioles** and **capillaries**. The

liquid part of the blood is called **blood-plasma** so long as it is contained **within the blood vessels**, and **lymph** as soon as it has seeped through the walls of the blood vessels and bathed the surrounding tissues. It is gathered up from here by the various lymphatic vessels which unite to form the large **lymph duct**. This duct empties into one of the veins of the neck. The blood, which has remained within the blood vessels and passed through the capillaries, is taken up by the venous capillaries and passes toward the heart either directly or indirectly through a **portal system**.

It is essential that one appreciate that the arteries **supply** all parts of the body with nourishment and that the veins do the **draining**. It follows, then, that the arteries begin as vessels of some size and become smaller and smaller as the blood supply from the heart becomes distributed more and more, while veins begin as capillaries and continually increase in size. An artery and a vein often lie side by side, but the **blood current** in the vessels is running in an opposite direction.

In addition to the systemic circulation there is also the **pulmonary circulation**, which is the name given to the blood stream leaving the right ventricle of the heart, passing through the **pulmonary arteries** to the lungs, and after being aerated, **returning through the pulmonary veins** to the left auricle, from whence it flows downward into the left ventricle to be ready again for the systemic circulation.

Whenever a vein splits up into capillaries so that the venous blood must pass through an organ on its way back to the heart (either to have waste substances removed, as in the kidneys, or to take up new substances as in the liver), and this blood is then again collected by venous capillaries and sent on its way, a **portal system** is formed.

The **renal-portal** system and the **hepato-portal** system are the two important ones in the economy of man's body.

When the circulatory system of the frog was discussed, it was stated that one must not forget that the material with which the heart works is **blood**, but that the heart is similar to a pump or an engine, and, that, consequently, just as a pump or an engine which is used for the purpose of forcing water through a great hydraulic system requires water in two places and in two ways to continue its work, so the heart requires blood in two places and in two ways to do its work.

The engine requires water in its boiler so that steam can be produced. This steam then supplies the force for its work of pumping water, let us say, through the water-pipes of the building in which it is installed. So, too, the heart must have a blood supply to furnish it with energy just as the engine requires water to manufacture its steam. Therefore, there are blood vessels running into the heart-walls and into the walls of blood vessels themselves so as to furnish these with material to produce the required energy to continue their pumping power. The blood vessels that supply the heart walls are known as **coronary vessels**.

The coronary arteries leave the aorta immediately after the aorta, in turn, has left the left ventricle. The blood vessels in the walls of blood vessels are known as **vasa-vasorum**.

It is essential that these two systems be kept separate and distinct. The mere pouring of blood into the cavities of the heart is equivalent to the water in the tank of an hydraulic system, while the blood which enters the heart muscle itself is equivalent to the water in the engine's own boiler that furnishes the steam from which the energy, in turn, comes to make pumping possible.

This analogy may be carried a little further; for, just as the water in the hydraulic system, if it be used for drinking purposes, must be **filtered**, so, before the blood, which is pumped through the vascular system, can be used again, it must likewise be filtered. This is the work of the **portal systems**.

A final point to be borne in mind, before taking up the circulatory system in detail, is that the **vertebrate circulatory system** is known as a **closed circulation**, as distinguished from the **open system** seen in some of the lower forms of animals, such as the crayfish.

What is meant by a **closed system**, is that the blood from the time it leaves the heart until it returns, is always in **direct communication** by means of arteries, capillaries, and veins. There are no open spaces through which the blood can pass out of these vessels. A seeming exception is the lymph. This does not pass through an opening, however, but seeps directly through the walls and bathes all parts of the **inter-capillary region**.

## DEVELOPMENT

It is well known that the mammalian heart has its point, or apex, to the left, but the student must know how this has come about. He must also know why it is that, just as with the digestive tract, certain nerves which lie in the right and left side of the early embryo, come to lie on the dorsal and ventral sides in the adult. The heart, like the digestive tract, grows something on the order of a straight tube, although made up of separate cephalic and caudal ends which have become fused together. As the embryo continues developing, the heart turns to the left, so that the nerves, which lie upon the right side, will now be ventral, and those which lie upon the left side will be dorsal, while the right auricle and ventricle, which have been brought ventral by this turning, to the left now occupy almost the entire ventral portion of the heart, the left auricle and ventricle being dorsal. It is for this reason that but a very small portion of the left auricle and ventricle can be seen from the ventral side of the body. It will be remembered that in the embryo of the chick mention was made of mesoblastic cells which were derived from three separate sources. One source of these is from the primitive streak. The second source is from that scattered group of cells left

between the ectoblast and entoblast when the entoblast became a distinct layer of cells. Thirdly, in the middle and lateral parts of the area pellucida, cells are budded off from the upper side of the entoblast to become mesoblast, at about the time the primitive streak is forming.

Now, all of these mesoblastic cells together unite to form a continuous layer. This layer continues expanding until it passes beyond the boundaries of the area pellucida and forms a middle layer in the inner zone of the area opaca. This zone is the **vascular area** (Fig. 264). It is in this area that the blood vessels begin to form. This occurs in the chick on the very first day. A network appears in the entire vascular area which surrounds the embryo. Here irregular reddish blotches are formed, called **blood islands**; it is from these blood islands that the red corpuscles are formed. This network develops into a system of cords, at first solid; but soon a **lumen** is acquired and, as the vessels unite, a continuous, but indefinite, blood vessel is formed. The very first vessel which becomes definitely shaped so that it can be recognized as a part of the vascular system is formed around the entire vascular area as a sort of boundary and is called the **sinus terminalis** (Fig. 284, C).

The blood islands appear in cross section as little local thickenings on the dorsal walls of the blood vessels. These bud off into the cavities of the vessels and form the first blood corpuscles, and it is supposed that from these all the colored corpuscles of the blood are descended.

The network of vessels continues to grow, some of the vessels later becoming arteries, some veins, and still others remaining small as capillaries. These unite and extend **toward the embryo**, while, within the embryo proper, there has been a growth of the vascular system also, which has extended outward **toward this vascular area**. All these vessels unite to form the entire vascular system.

Larger vessels of the vascular area unite with the posterior end of the heart which by this time has already begun to beat. The other vessels unite with the anterior, or cephalad, end of the heart and become the arterial system, so that by the end of the second day, in the chick, a complete vascular system has already been formed with a beating heart.

At first the heart consists of only two longitudinal vessels which are connected at the cephalic end. These spread out caudad like an inverted "V" (Fig. 283). The arms of this "V" shaped portion soon fuse together and look like an inverted "Y." The cavities of these two fusing tubes remain apart for some time and then form **one cavity**. That is, the endothelial lining remains separate as two distinct cavities for a time, even after the muscular walls have united.

On the dorsal surface, the muscular walls are incomplete also for a short time, but after complete fusion the walls also are completed. It is the stem of this "Y" which forms the heart. The two diverging arms of the "Y" unite, or rather have united some time before this, so that

they are continuous with the large **vitelline veins** which bring the blood back to the heart from the vascular area.

The heart is now a **short straight tube** attached to the ventral wall of the pharynx and consists of the muscular united part of this "Y," the two arms are the ends of the diverging vitelline veins which run backward or caudad at the hindermost angle of the head fold. As this fold is pushed farther and farther back, the straight part of the "Y" is naturally pushed back also and lengthened. Not only this, but this **straight part of the heart grows more rapidly** than does the place to which it is attached, so that it does not even find room enough to continue its growth with the heartfold, but must bend into a loop with its convexity toward the right side of the embryo. The heart has now lost its attachment to the pharynx (with exception of its two ends). The

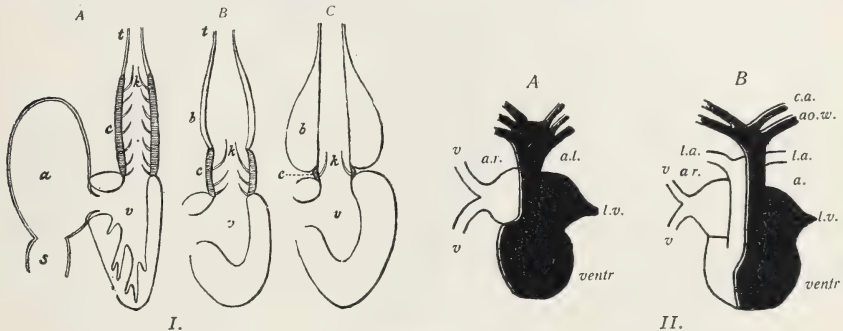


Fig. 446.

I. Schematic longitudinal sections of the heart. *A*, dogfish, *B*, Ganoids, and *C*, Teolosts. *a*, atrium; *b*, bulbus arteriosus (an enlarged portion of the truncus arteriosus); *c*, conus arteriosus; *k*, valves; *s*, sinus venosus; *t*, truncus arteriosus; *v*, ventricle. (After Boas.)

II. The circulatory system in the amphibians. *A*, *Urodele*, and *B*, *Anura*. *a.l.* and *a.r.*, left and right atria; *ao.w.*, aortic root (radice); *ca.*, carotid arteries, which spring from the conus arteriosus together with the *ao.w.*; *l.a.*, pulmonary arteries which carry venous blood from the ventricle to the lungs; *l.v.*, pulmonary veins which carry arterial blood to the left atrium; *v*, the veins which carry venous blood from the general body system to the right atrium; *ventr.*, ventricle. (From Schimkewitsch after Wiedersheim.)

caudal end of the heart, in which the vitelline veins empty, is called the **venous** and the cephalic end is spoken of as the **arterial end** of the heart. The beating of the heart begins as soon as a connection has been made between this "Y" shaped tubular vessel with the vessels which have been formed in the vascular area. The palpitation starts at the venous, or caudal, end and passes to the arterial, or cephalic, end. The palpitation of the heart already begins before one can distinguish any definite muscular tissue which has developed from the mesoblast.

The arterial end of the heart is known as the **bulbus arteriosus**. From this, two narrow vessels, the aortic arches, pass around the digestive tract to the dorsal side, turning caudad and becoming the **dorsal aortae**. These two dorsal aortae run along each side of the notochord under the mesoblastic somites and pass toward the tail unconnected

with each other, but just before reaching the tail, a large branch is given off. In fact, the branch is much larger than the aorta itself from which it arises. This large branch is called the **vitelline artery**. The vitelline arteries carry the blood back to the vascular area from which it was brought by the vitelline veins.

The heart we have just been describing is that of the chick. In cyclostomes and fishes (except the dipnoi) there is what is known as a **branchial, or venous, heart** (Fig. 446). All of the blood which enters such a heart is venous blood. This venous blood is pumped directly to the gills where it loses its carbon dioxide and takes up oxygen before being distributed to the various parts of the body. The important thing to note is that in such cases the blood only passes through the heart **once** in making its complete circuit. It is not, however, correct to consider the embryo of higher forms as being the same as this type of "one-heart-circulation," for only oxygenated blood passes through the heart in such embryos when it is in this stage.

In the dipnoi and amphibia (Fig. 446), where lungs are formed to take up part of the work of the gills, the heart divides in an **arterial, or systemic, and a venous, or respiratory, half**. This division is caused by a **septum**, or partition, in the auricle which divides the chambers. It will be remembered that blood always enters through a vein and always enters into a sinus or an auricle of the heart. The venae cavae

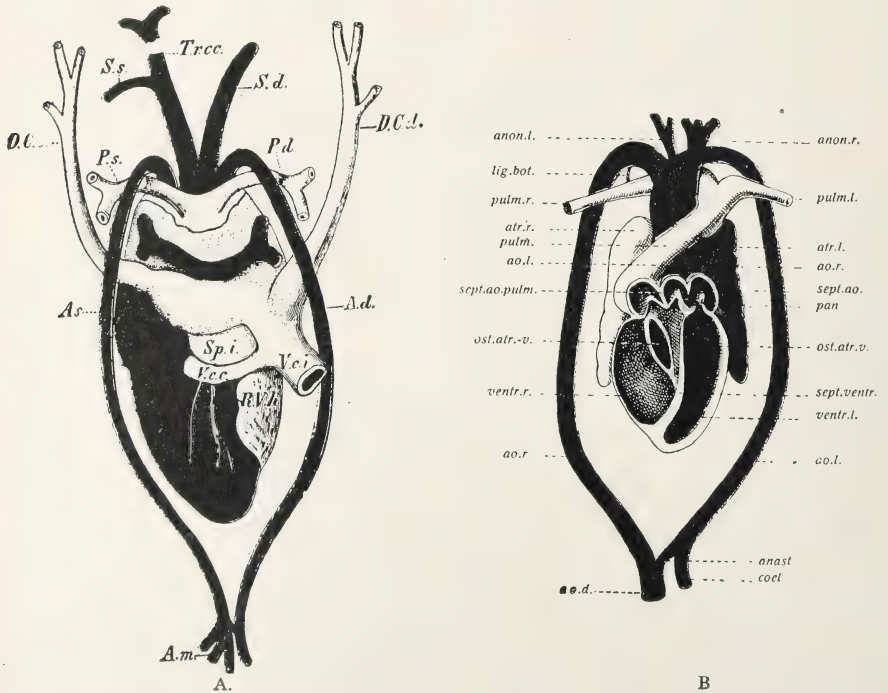
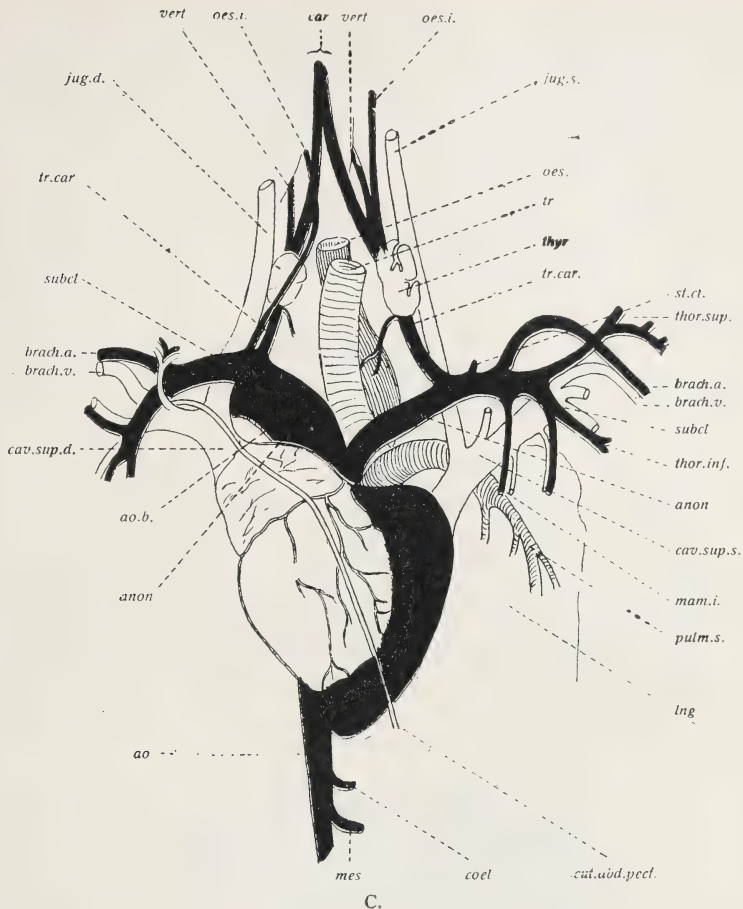


Fig. 447.



Comparisons of heart and connecting blood vessels in the crocodiles and birds. *A*, Dorsal view of Crocodilian heart. *A.M.*, mesenteric artery; *Ad* and *As*, aortic arches; *D.C.d.* and *D.C.s.*, right and left ducts of Cuvier; through which the venae cavae enter the heart; *LV.*, pulmonary veins; *LV.h.* and *RV.h.*, left and right atria; *P.d.* and *P.s.*, right and left pulmonary arteries; *S.d.* and *S.s.*, right and left subclavian arteries; *Sp.s.*, region of the interseptal valves; *Tr.cc.*, common carotid artery; *V.c.c.*, Coronary vein; *V.c.i.*, inferior venacava. (After Rose.)

*B*, Ventral View of Crocodilian Heart. *anast.*, so-called dorsal anastomosis of the two roots of the aorta; *anon.l.* and *anon.r.*, left and right innominate trunks; *ao.l.*, left aortic arch; *ao.d.*, dorsal aorta; *ao.r.*, right aortic arch; *atr.l.* and *atr.r.*, left and right atria; *coel.*, coeliac artery; *lig.bot.*, Botalli's Ligament; *ost.atri.v.*, atrio-ventricular opening; *pulm.*, pulmonary artery; *pan.*, foramen of Panizzae; *sept.ao.*, aortic septum; *sept.ao.pulm.*, aortic-pulmonary septum; *sept.ventr.*, ventricular septum; *ventr.l.* and *ventr.r.*, left and right ventricle. (After Greil.)

*C*, Heart and communicating vessels of bird. (Swan.) *anon*, innominate artery; *ao*, aorta; *a.o.b.*, aortic arch; *brach.a.* and *brach.v.*, brachial artery and vein; *car*, carotid artery *car.sup.a.* and *car.sup.s.*, right and left superior venae cavae; *coel*, coeliac artery; *cut.abd.pect.*, cutaneous abdominal-pectoral vein; *jug.d.* and *jug.s.*, right and left jugular veins; *lng*, lung; *mam.i.*, internal mammary artery; *mes*, mesenteric artery; *oes*, oesophagus; *oes.i.*, inferior oesophageal artery; *pulm.s.*, left pulmonary artery; *st.cl.*, sternoclavicular artery; *subcl.*, subclavian artery; *thor.inf.* and *thor.sup.*, thoracalis inferior and superior arteries; *thyr*, thyroid gland; *tr*, trachea; *tr.car.*, carotid trunk; *vert*, vertebral artery. (After Gadow.)

which return the systemic blood to the heart, therefore, empty into the right auricle, while the pulmonary veins which carry blood from the lungs to the heart enter the left auricle. As this blood which has returned from the lungs is now oxygenated and ready for distribution to the general system, it is the **left side** of the heart which becomes the **arterial side**.

In the higher forms, the ventricle is also divided by a septum. The valves on the right side which separate the auricle from the ventricle are called the **tricuspid valves**, while those on the left side separating the left auricle and left ventricle are known as the **mitral**, or **bicuspid**, valves.

In the crocodiles, there is an opening between the two sides of the aortic trunk, known as the **foramen Pannizae** (Fig. 447, B. pan), so that there is really some mixture of arterial and venous blood in these animals.

The separation into **four compartments** is complete in birds and mammals (Figs. 445, 447, C), so that the blood must pass through the heart twice—once through the venous, and once through the arterial half—in order to make a complete circuit of the body.

The heart is formed directly behind the mandibular artery which is the first aortic arch (Fig. 309), so that as other vessels grow, it is forced back further and further until it lies ventrad and caudad to the pharynx; while in the adult higher forms of mammals, it is carried back as a result of this unequal growth even into the thorax. (The extreme of such migration is seen in the giraffe and the long-necked birds.)

## THE ARTERIES

### AORTA AND AORTIC ARCHES

The ventral aorta is that large artery running headward from the heart. It extends to the mandibular artery which is another name for the first aortic arch (Fig. 309). The mandibular arteries, like other arches, pass dorsad (one on each side of the pharynx) until they meet and form a pair of dorsal longitudinal tubes called the **radices aortae**. Between the first aortic arch (mandibular artery) and the heart there arise some six or more pairs of arches similar to those forming the mandibular artery. The number of such arches depends upon the number of gill-clefts the animal has, for these arches develop in the septum between the gill-clefts. (The number of arches is greater in the myxinoids where the number of clefts varies; seven or eight in the notidanid sharks; and, as recent investigations tend to show, probably six in the embryos of all other vertebrates.)

As the embryo continues to grow, the number of these arches, which remain or degenerate, seems to be influenced to a considerable extent by the various changes of the respiratory system, which the particular

animal in question may develop. When gills develop, each aortic arch divides into two portions: an **afferent branchial artery**, which carries the blood from the ventral aorta to the gills, and an **efferent branchial artery** which carries it from the gills to the radix aortae. Both afferent and efferent vessels run parallel to each other for a part of their course, and are connected with each other by numerous capillary loops running through the gill filaments. As the blood passes through the gills, it loses its carbon dioxide and takes up oxygen so that it is changed from venous to arterial blood. In all animals that develop an amnion, one cannot distinguish between afferent and efferent branchial arteries, the aortic arches running directly from the ventral aorta to the dorsal longitudinal radices aortae.

With the possible exception of cyclostomes, no gills are ever developed in the region of the first arch, so no afferent and efferent vessels

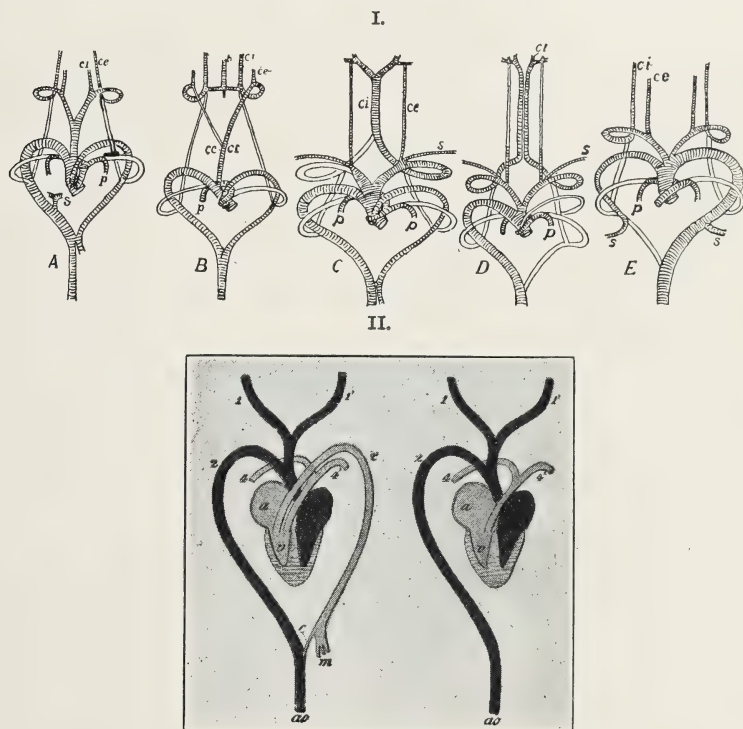


Fig. 448.

I, Aortic arches of amniotes. Compare with Figure 309. *A*, African Lizard (*Varanus*); *B*, Snake; *C*, Alligator; *D*, Bird; *E*, Mammal. *b*, basilar artery; *ec*, common carotid; *cei*, *ce*, internal and external carotids; *da*, dorsal aorta; *p*, pulmonary; *s*, subclavian. (From Kingsley after Hochstetter.)

II, Comparison of Heart and aortic arch of crocodile and bird. *a*, right auricle; *a'*, left auricle; *ao*, descending aorta; *c*, small connecting vessel; *m*, intestinal branches. (*c* and *m*, before they separate, form the left aortic arch); *v*, right ventricle; *v'*, left ventricle; *1* and *1'*, carotid arteries; *2* and *2'*, right and left aortic arch; *4* and *4'*, pulmonary arteries. The right aortic arch, together with the tiny branch, *c*, forms the descending aorta. (After Boas.)

arise from the mandibular arteries. There is, however, an external and internal **carotid artery** which supply the head and brain, which come from each half of this first arch (Fig. 448). As various changes take place, however, the relation of the carotids makes them appear as though they arose from the first functional arch.

In the cyclostomes and fishes, the various arches do not undergo much, if any, modification. Whatever modification does occur depends upon changes in the gills.

In all land vertebrates and many of the fishes, the first arch on both sides disappears at the point where the external carotid artery begins.

When the spiracular gill is reduced, the second pair of arches is partially or completely lost in the adult.

The third pair persists. The blood for the **internal carotids** flows through these. In fishes, gymnophiona, and a few urodeles, the blood for the radices aortae also flows through the third pair. In all four-footed animals, the radix disappears between the third and fourth arches so that it leaves the third arch purely carotid. In such a case that part of the ventral aorta, which is between the third and fourth arches, carries the carotid blood along and hence is known as a common carotid artery (Fig. 448, I, B). This usually divides into a right and left branch later.

The fourth pair form the **systemic trunks** in all four-footed animals and carry blood from the ventral to the dorsal aortae.

The fifth has become smaller and disappears in nearly all animals except lizards and urodeles. In reptiles the left side of the fourth arch becomes separated from the rest of the ventral aorta, having its own trunk connected with the right side of the partially-divided ventricle, thus carrying a mixture of arterial and venous blood. The blood from the left fourth arch on the dorsal side is largely distributed to the digestive tract. The right side of the arch and the carotids are connected with the left side of the heart and are consequently purely arterial, the arch itself forming the main trunk which connects the heart with the dorsal aorta. In birds, the radix on the left side of the adult disappears caudad to where the subclavian artery begins so that this arch supplies blood only to the left arm. The right arch is purely aortic in character. **In the mammals, this is entirely reversed; the right arch is subclavian and the left supplies the dorsal aorta and the subclavian of that side.**

The bird in its embryonic growth (as exemplified by the chick embryo), turns upon its left side in about 80 per cent of all cases, and the right arch persists, while in mammals, the embryo usually turns upon its right side and the left arch persists.

When lungs are developed, whether that be in the lung fishes or any of the higher forms of animals, a pair of **pulmonary arteries** develop from the sixth pair of arches on the ventral side of the pharynx. These arteries grow caudad into the lungs. That part of the arch dorsal to these newly formed pulmonary arteries becomes reduced to a small

vessel known as the **ductus arteriosus**, or the **duct of Botallus** (Fig. 345), C, d, b) in some of the urodeles. In some of the higher vertebrates, one occasionally finds a persisting vestige of this, otherwise it entirely disappears.

The ductus Botalli is quite important in the embryonic circulation of amniotes, because the greater part of the blood goes through it to reach the dorsal aorta during the time the allantois is the organ of respiration, while only enough blood goes through the pulmonary artery to nourish the lung. The duct closes with the first inspiration of air, while all blood passing into the last arch goes to the lung.

In the lung fishes and amphibia, where there is but a single ventricle in the heart, the pulmonary arteries are connected with the ventral aorta just as are the other aortic arches. In higher forms, however, such as the amniotes, where there is either a partial or complete division of the

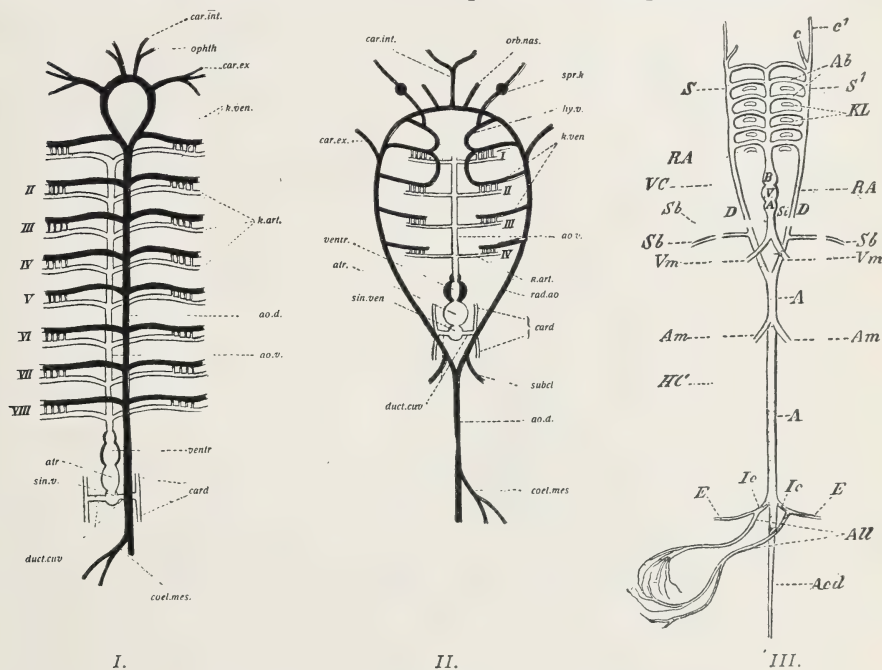


Fig. 449.

Schematic diagrams of circulatory systems in I, *Petromyzon*, II, *Teleosts*, III, in the higher vertebrates. I to VIII, gill arches; A, atrium; Ab, gill veins; Acd, caudal artery; All, allantoic artery; Am, omphalo-mesenteric artery; RA, and rad.ao., Aortic radices (roots of the aorta); S, S', two branches; card., anterior and posterior cardinal veins; car.ex., c, and car.int., c' external and internal carotid arteries; coel.mes., coeliaco-mesenteric artery; duct.cuv., and D, duct of Cuvier; E, external iliac artery; HC, posterior cardinal vein; Ic, common iliac artery; hy.v., gill veins of the hyoid arch; k.art., gill arteries; k.ven., gill veins; KL, gill clefts; ophth., ophthalmic artery; orb.nas., orbito-nasal artery; RA, and rad.ao., Aortic radices (roots of the aorta); S, S', two branches of the gill veins which pass into the aortic radices; Sb, Sb, and subl., subclavian artery; Sb', subclavian vein; si, and sin.ven., sinus venosus; spr.k., spiracle gill; v, and ventr., ventricle; VC, anterior cardinal vein; Vm, omphalo-mesenteric vein. (From Schimkewitsch, I, after Vogt, Jung and Bridge; II, Parker; III, Wiedersheim.)

ventricle into two portions, the **conus arteriosus** and the ventral aorta are divided so that those portions, which are derived from the sixth arch are connected with the right side of the heart, while the rest of the ventral aorta, with the exception already noticed in the reptiles, receives its blood from the left side of the heart.

It is necessary to study the figures very carefully in order to see how, even in the vertebrates such as the elasmobranchs, there is a differentiation of the fifth and sixth arches from the rest of the series. It will be remembered that the fifth arch is almost completely obliterated in vertebrates possessing lungs, and that the sixth is completely separated from the rest.

The dorsal aorta comes into existence by the fusion of two primitive vessels running caudad. These lie dorsal to the mesentery and run almost parallel to the notochord to the very end of the body. This fusion varies; it may extend as far forward as the aortic arch. It will be remembered that the portions which would normally be called the dorsal aortae, when these segment or when there is a division between the various arches, are called **radices aortae**. Sometimes the dorsal aortae extend still farther forward than the last aortic arch and involve the whole of the radices, so that the dorsal aorta in this case extends to the first arch.

Students of comparative anatomy who are preparing for medicine, dentistry, and other professions, should note the fact that the names in human anatomy are somewhat different from those adopted in books on comparative anatomy. In the study of human anatomy that part of the ventral aorta which persists is called the **ascending aorta**; that part of the fourth arch, which continues in existence, is known as the **arch of the aorta**; and the rest of the dorsal aorta, running downward toward the feet, is called the **descending aorta**. This, in turn, is divided into one portion (passing into the thorax) known as the **thoracic aorta**, while from the diaphragm downward (as it passes into the abdominal cavity) it is known as the **abdominal aorta**. The last two names are thus only convenient terms to show the location of the descending aorta.

## ARTERIES OF THE DORSAL AORTA

These are known as **visceral (splanchnic)** and **somatic**. As these terms are already familiar to the student, it is merely necessary to state that the visceral arteries run through the mesenteries, where the double layers of serosa are found, to furnish the blood supply of the digestive tract. Many of the blood vessels are in a primitive condition, though they are not metameric. Usually, especially in vertebrates, these smaller vessels become united into larger trunks. The principal ones are as follows:

## VISCERAL ARTERIES (Fig. 444)

### Coeliac Artery:

**Origin**, Radix or adjacent dorsal aorta.

**Branches**, Gastric, splenic, hepatic.

**Superior Mesenteric Artery** (running to cephalic portion of intestines). Develops with the omphalomesenteric.

**Inferior Mesenteric Artery** (to caudal portion of intestine).

(Not always present. Other mesenteric arteries may also appear.)

**Coeliac Axis**—is the name applied if the superior mesenteric fuses with the coeliac artery.

### Hypogastric Arteries:

Originally connect dorsal aorta with subintestinal vein near anus, later supplying rectum.

In animals higher than vertebrates, a urinary bladder grows from the rectal region, which is supplied by hypogastric branches called **vesical arteries**.

In amniotes, where the proximal end of the allantois becomes the bladder, parts of the vesical arteries become **allantoic arteries** or **umbilical arteries**, because they pass through the umbilicus. With the disappearance of the allantois, these arteries degenerate, leaving only the rectal and vesical branches of the hypogastric trunk.

### Caudal Aorta:

That portion of the dorsal aorta caudad to the hypogastric arteries.

## SOMATIC ARTERIES

Distributed to the body wall and its derivatives. (Unlike the visceral arteries, the somatic arteries are arranged metamerically.)

### Intercostal Arteries (Fig. 444):

One pair develops between each pair of myotomes, beginning at the radices and the dorsal aorta. As the aortic arches disappear and change, the intercostals become connected close to their origin by a pair of vertebral arteries running through the openings in the transverse processes of the vertebrae. The intercostals have different names, depending on their location, as **thoracic**, **lumbar**, **sacal**, etc.

### Vertebral Arteries:

In both man and other vertebrates, the vertebral arteries pass in a cephalad direction toward the ventral side of the medulla oblongata where the right and left arteries unite to form one trunk called the **basilar artery**. This runs straight forward underneath the brain. Two branches of the vertebrals extend caudad from points just before where the two vertebrals unite.

### Circle of Willis:

Just before the basilar artery reaches the **hypophysis** (pituitary body), it divides, so that one-half of the basilar passes on each side of the hypophysis. The **internal carotid artery** meets this divided basilar on each side, and the trunks thus formed meet near the **optic chiasma**, forming a complete **arterial ring** called the **circle of Willis**. It will be noticed that the brain has thus a supply of arterial blood from both ventral and dorsal regions, making it less likely to suffer from anything that might impede the circulation in any one part.

### Subclavian Arteries:

As the limbs grow, a segmental artery, for each somite concerned in the appendages, extends into the member. These arteries become connected with each other distally, as well as with the veins of the limb, by a network of small vessels. The parts of these main trunks and the connecting network enlarge while other portions atrophy. There are numerous variations in the blood supply of the limbs. This explains the shiftings of the subclavian artery shown in Figure 448.

The subclavian has the following names applied to different portions:

**Axillary**—that part lying in the axilla.

**Brachial**—that part lying in the upper arm.

**Radial and Ulnar**—the parts lying adjacent to the bones of these names.

### Epigastric Arteries:

The development of the arteries of the hind leg is somewhat complex. There is the same formation of a capillary network as with the fore-limb. Two of the arteries become prominent. The **epigastric artery** lies forward. It descends from the aorta to the ventral side of the body and forward to supply the lower portion of the myotomes. It becomes connected with the epigastric veins at first, although later these may anastomose with the hinder ends of the cutaneous arteries. When the hind limb grows out, the **external iliac, or femoral, artery** (a branch of the epigastric), is sent into its anterior side. As the leg increases in size this sometimes surpasses the parent epigastric in size, so that the latter appears as a mere side branch.

### Sciatic Arteries:

The **sciatic or ischiadic arteries** descend into the posterior side of the leg, the name changing at the angle of the knee to **popliteal artery**. Farther down, this artery divides into **peroneal** and **anterior** and **posterior tibial arteries**. The peroneal supplies the calf of the leg and the others continue into the foot.

The arrangement of vessels here outlined is characteristic of the

lower tetrapoda where the femoral artery is small. It is likewise characteristic of the embryos of mammals. In the latter, however, before birth, the femoral artery grows down to join the popliteal, and so becomes the chief supply of the limb. These trunks and the hypogastric do not always remain distinct. They often fuse in different ways at the base. Epigastric and hypogastric arteries are distinct in many reptiles and in birds, but in other vertebrates they fuse to form the **common iliac artery**, so called because the proximal portion of the femoral is often called the **external**, and the hypogastric the **internal iliac artery**. The sciatic, likewise, may remain distinct, or it may fuse with the others at the base, but then its independent portion will appear as a branch of the common iliac artery.

A **cutaneous artery** arises from either the subclavian or the pulmonary artery of either side (both conditions occur in the amphibia) to run backward in the skin of the trunk. It may extend back and unite with the epigastric artery. If, as in amphibia, these arise from the pulmonary artery, they contain venous blood and the skin acts as a subsidiary respiratory organ.

#### **Renal Arteries:**

Renal arteries are paired and show metamerism in the primitive state. Details of this are given in the description of the organs they supply. It is well to note that metamerism is well shown in these arteries going to the pronephros and the mesonephros, while in the true kidney—the metanephros—only a single pair of renal arteries furnishes the blood supply.

#### **Genital Arteries:**

These, like the renal arteries, are paired and metameric in the primitive state and are called

**Spermatic** in the male.

**Ovarian** in the female.

These are more numerous in lower animal forms than in higher.

## **THE VEINS**

#### **Omphalomesenteric Veins:**

It will be remembered that the heart is developed in the pericardial cavity. Caudad to the heart region, the liver begins developing and thus prevents the lateral plates from coming together on the ventral side as they did in the case of the heart. The lateral plates, however, become grooved, and each one forms a tube, so that there are two vessels, called the **omphalomesenteric veins** extending caudad from the heart, passing around the liver where they meet with the extensions of the omphalomesenteric **arteries** already described (Fig. 277).

## Subintestinal Veins:

Caudad to this connection a pair of **subintestinal veins** (Fig. 450) run toward the tail end on the ventral side of the digestive canal. These fuse together into a medial tube just behind the anal opening; this tube

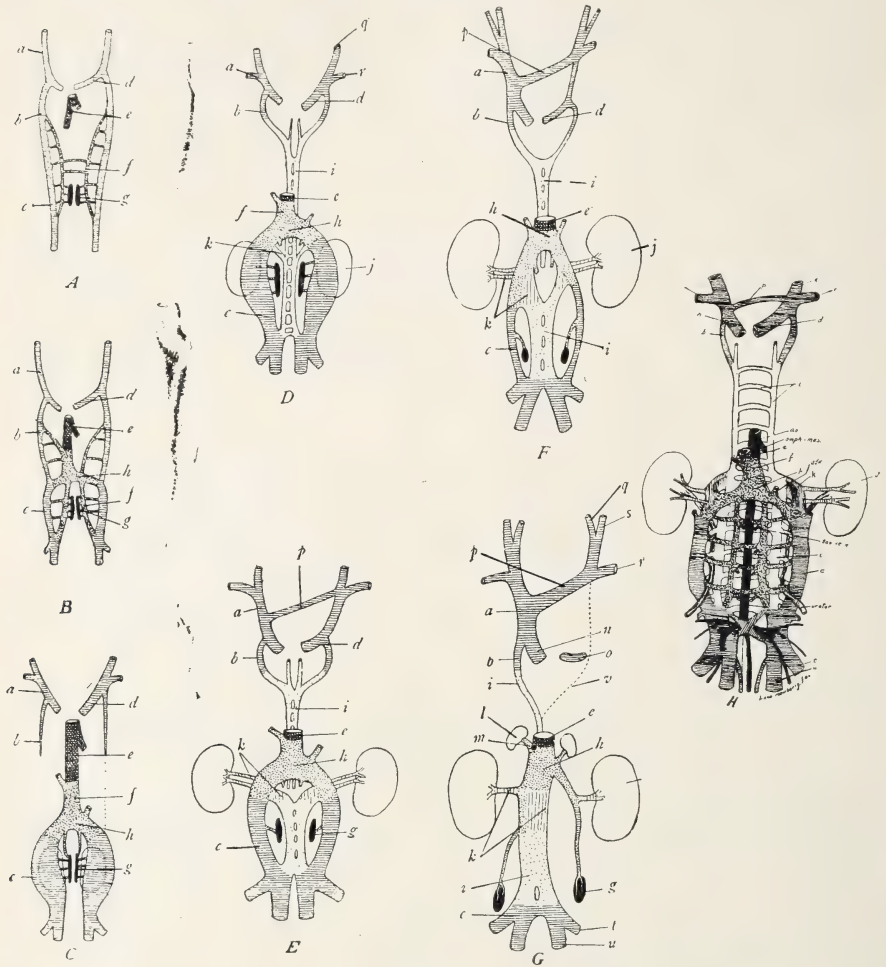


Fig. 450.

Diagrams to show the development of the postcaval vein in the cat. The *cardinal* system of veins is cross-hatched, the *subcardinal* veins closely stippled, the *hepatic* veins are indicated by cross, vertical, and oblique hatching combined, the *supracardinal* veins by open stippling, and the *renal collar* by vertical hatching.

A, early stage, showing the anterior and posterior cardinal veins, *a*, *b*, *c*, the common cardinal vein *d*, the subcardinal veins *f*, and the outgrowth *e* from the hepatic veins of the liver. B, next stage, showing the union of the hepatic outgrowth *e* with the subcardinal veins *f*, to form the proximal part of the postcaval vein; the two subcardinals have united with each other at *h*.

C, the anterior part of the posterior cardinal vein *b* has separated from the posterior part *c*, *c* now being the renal portal vein; the postcaval vein is seen to be formed of the hepatic vein *e*, the right subcardinal *f*, and to be united by means of the two subcardinals below *h* with the renal portals *c*.

D, the supracardinal system of veins *i*, represented by open stippling, has ap-

extends to the end of the tail. This fused portion is known as the **caudal vein**. In the cyclostomes this connection persists. It disappears in other vertebrates.

The left omphalomesenteric vein, which passes along the left side of the liver, continues to carry blood from the caudal or posterior part of the body to the heart, while the right disappears with the exception of the small portion between the sinus venosus and the liver.

### The Portal System:

It will be remembered that the liver develops from a simple sac into a compound, tubular glandular structure. The left omphalomesenteric breaks up into a great mass of capillary-like tubules or **sinusoids**, which pass among the tubules of the liver and end by reconnecting at the cephalic end of the liver. As the liver increases in complexity so do these sinusoids. The left omphalomesenteric is consequently quite important during this period and is known as the **ductus venosus (Arantii)**, (Fig. 451). A little later, however, this importance is lost by a part of the omphalomesenteric becoming the **portal vein**, which brings all the blood from the posterior regions of the body to the liver, sending it through the tiny sinusoids. The ends between the heart and the liver, formerly called the **ductus venosus**, now become the **hepatic veins**. It is in and through the hepatic veins that the collected blood from the liver sinusoids is sent to the heart.

When a vein breaks up into capillaries of this kind, as in the liver and kidneys, and its contents are again gathered in a vein, it is called a **portal system**. That of the liver is the **Hepatic portal**, while that of the kidney the **Renal portal system**.

In elasmobranchs and sauropsida, which produce eggs with large

peared and has united anteriorly with the anterior parts of the posterior cardinals *b*, medially with the subcardinals by an anastomosis *k*, named the renal collar, and posteriorly with the renal portals *c*.

*E*, union of the two anterior cardinals by a cross-connection *p*, and development of the renal veins from the renal collar *k*; the supracardinal veins have separated into anterior parts connected with the posterior cardinals *b* and posterior parts connected with the subcardinals and renal portals *c*.

*F*, continuation of *E*.

*G*, adult stage; the left anterior cardinal joins the right by means of the cross-vein *p* which is the left innominate vein; the common stem *a*, which is the right anterior cardinal, enters the heart by way of *n*, which is the right common cardinal vein; the left common cardinal vein persists as the coronary sinus *o*; the right anterior parts of the posterior cardinal vein and supracardinal form the azygos vein, *b* and *i*, while on the left side these are obliterated at *v*; the postcaval vein is now complete and is seen to be composed of the hepatic vein *e*, the right subcardinal, the anastomosis between the two subcardinals at *h*, the right renal collar *k*, the posterior part of the supracardinal vein *i*, and the posterior parts of the renal portals (posterior cardinals) *c*; the left subcardinal and posterior cardinal contribute to the vein of the left gonad, hence the symmetrical arrangement of the genital veins in mammals.

*H*, composite diagram of the veins of a cat. *a*, anterior cardinal; *b*, anterior part of the posterior cardinal; *c*, posterior part of posterior cardinal or renal portal; *d*, common cardinal; *e*, hepatic portion of the postcaval (this is partly removed in Figs. *D-G*); *f*, subcardinal; *g*, gonad; *h*, union between the two subcardinals; *i*, supracardinal; *j*, kidney (metanephros); *k*, renal collar or union between subcardinals and supracardinals; *l*, adrenal gland; *m*, vein to adrenal gland; *n*, base of the pre-caval vein or right common cardinal; *o*, coronary sinus or left common cardinal; *omph.mes.*, omphalomesenteric artery; *p*, left innominate or connection between the two anterior cardinals; *q*, internal jugular; *r*, subclavian; *s*, external jugular; *t*, external iliac; *u*, internal iliac. (Partly from Hyman after Huntington and McClure in *Anatomical Record*, Vol. XX.)

yolk, the presence of a large food supply exercises a modifying influence on these ventral veins. A pair of large **vitelline veins** runs out into the yolk sac, over the yolk, from the junction of the omphalomesenteric and the subintestinal veins to play a large part in the transfer of material to

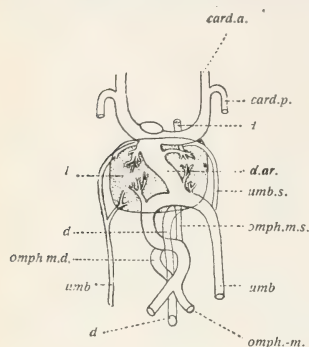


Fig. 451.

Diagram showing development of the mammalian hepatic portal system. The omphalo-mesenteric and the umbilical veins are reduced. *card.a.* and *card.p.*, anterior and posterior cardinals; *d.*, intestine; *d.ar.*, ductus venosus (*Arantii*); *l.*, liver; *omph.m.d.* and *omph.m.s.*, right and left omphalo-mesenteric veins; *umb.d.* and *umb.s.*, right and left umbilical veins. (After Hochstetter.)

the growing embryo (Fig. 284). The distal parts of these veins follow the margin of the yolk sac, forming a tube (**sinus terminalis**), into which smaller veins empty. Blood is brought to the yolk by the omphalomesenteric arteries. These arteries are also distributed to the yolk sac and divide up distally into a network of capillaries which connect distally with the vitelline veins. The blood is carried by these vitelline veins to the liver and through the portal circulation to the heart. A similar vitelline circulation is developed in the mammals, but here the yolk sac contains no yolk, and so is of minor importance and soon lost.

In amniotes there is an outgrowth, the allantois, which arises as a diverticulum from the hinder end of the alimentary canal. It increases in extent by growing downward and carrying the ventral body wall

before it. **Allantoic arteries** (branches of the hypogastric arteries) extend into it and are connected by capillaries with **umbilical veins** which arise from the subintestinal vein behind the vitelline veins. This forms an **allantoic circulation** which is both respiratory and nutritive in character. In the reptiles, both of the umbilical veins persist through foetal life, while in birds and mammals, one aborts, leaving the other as the efferent vessel of the allantois. With the end of foetal life (at hatching or at birth), both the vitelline and the allantoic circulations disappear, leaving only inconspicuous rudiments.

### Anterior Cardinal Veins (Superior Jugular or Jugular):

(The **inferior jugulars** are found only in fishes and salamanders, where they drain lateral and ventral branchial regions.) The superior jugular vein lies dorsal to the gill-clefts and returns blood from the dorsal regions of the head.

### Post-Cardinal Veins (Figs. 450, 456).

These are very clearly related in development with the excretory system and lie dorsal to the coelom and dorsal to the nephridial arteries. Nearly all of the thoracic portion of the post-cardinal veins soon disappears in the higher forms, while a **supra cardinal system** develops, as shown in Figs. 450, 456. This supra cardinal system in turn disappears

with the exception of a posterior portion which takes part in the forming of the post-cava, and the right anterior portion which connects with the remnant of the post-cardinal to become the **azygous** vein. If the anterior left side persists also, this is known as the **hemiazygous**.

In the lower vertebrates they retain their function of draining the excretory system.

### **Cuvierian Ducts:**

These are formed by the meeting of the anterior cardinal and the post-cardinal vein on each side to form short tubes for the emptying of the cardinal veins into the sinus venosus.

### **Subcardinal Veins:**

These are closely associated with the post-cardinals.

As the mesonephroi in their development reach the hinder end of the coelom, the caudal vein loses its primitive connection with the sub-intestinal vein and becomes connected with a pair of vessels, the **sub-cardinal veins**, which develop in a ventral-medial position to the two mesonephroi. The blood from the tail now goes through the sub-cardinals and from them into the excretory organs, passing through a system of capillaries to be gathered again in the post-cardinals and by them to be returned to the heart. Here, then, there is another portal system, the **first renal-portal system**, which may be modified later.

### **Subclavian Veins:**

One of these drains each forelimb. It originally empties into the post-cardinal but later may empty into the Cuvierian duct or jugular vein.

### **Common Iliac Vein:**

This drains the hind limb and empties into the epigastric (**lateral abdominal**) vein which in turn empties into the post-cardinal vein or duct of Cuvier.

This is the condition in some elasmobranchs, but in the reptiles and amphibia, the common iliac sends part of its blood as above, and part through the post-cardinal of its own side, so that blood from the hind limbs has two routes to the heart.

### **Anterior Abdominal Vein:**

The two epigastric veins in amphibia and some reptiles fuse in the midline to form an **anterior abdominal vein**, which passes through the remains of the ventral mesentery (**ligamentum teres**) to the liver and forward.

In one mammal, **Echidna**, alone has such an anterior abdominal vein been found.

The vessels of the appendages are but slightly developed in **fishes**. There is a subclavian vein which enters the Cuvierian duct, and some-

times a **branchial vein** which may empty into the sinus venosus. In the **amphibia**, a **cutaneous magnus vein** comes from the skin of the trunk, which may enter the subclavian. In all **tetrapoda**, the subclavian, after it leaves the limb, receives a superficial **cephalic** and an **axillary vein**. The latter, however, changes its name in the appendage to the **brachial vein**. The common iliac vein is formed in the limb by a union of the femoral and sciatic (ischadic) veins, as well as the **hypogastric** (internal iliac) vein.

In all classes above fishes, such as dipnoi, amphibia, and amniotes, a new vein, the **postcava (vena cava inferior)** arises in part from scattered spaces and in part as a diverticulum of the sinus venosus and the hepatic veins. It grows backward, dorsal to the liver, until it meets and fuses with the right subcardinal vein, a portion of which now forms a new trunk to carry blood from the posterior part of the body to the heart.

The following changes are introduced in the embryonic renal portal circulation whenever a postcaval vein develops: The subcardinals no longer connect with the caudal vein but are connected with each other by transverse vessels (**interrenal veins**). Portions of the post-cardinals grow backward to connect with the caudal vein. These posterior parts of the post-cardinals then become the **advehent veins** (Fig. 452) of a

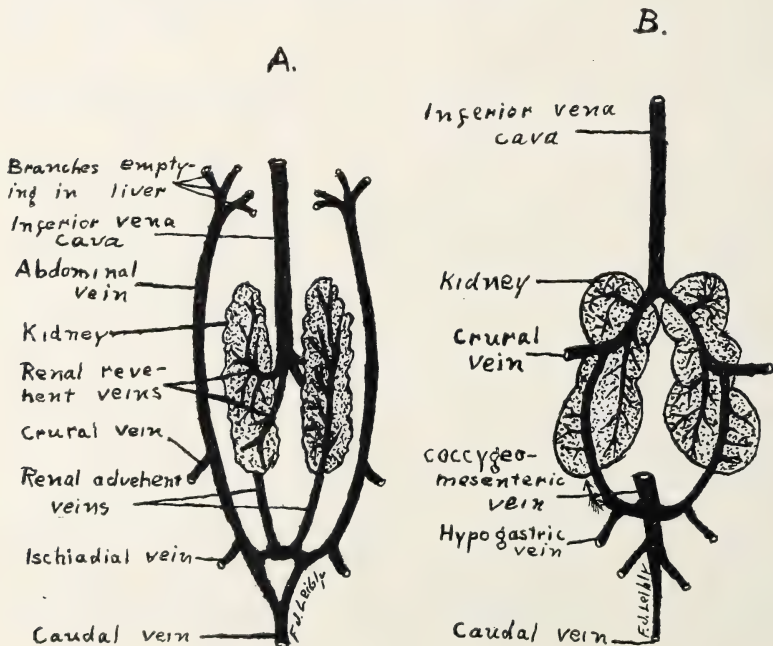


Fig. 452.

Diagram of Renal Portal System in A, Alligator, and B, Bird. (After Gegenbaur.)

second renal portal system. They bring blood from the tail and hind limbs to the excretory organs (mesonephroi). The subcardinals of both sides usually fuse in the middle line. The fusion is initiated by the appearance of the interrenal veins, which now act as **revehent vessels** to carry blood from the excretory organs to the postcava and to the anterior portion of the post-cardinals which have joined the anterior ends of the subcardinals. In mammals there is also a change in the post-cardinals and in the renal portal system.

In the lung fish, **Ceratodus**, there are some differences from the foregoing changes. Here the cephalic portion of the right post-cardinal loses its connection with the vessels behind, and acts as a **vertebral vein**, taking the blood from the intercostal veins of that side back of the heart. The caudal and the subcardinals form a continuous trunk, while the revehent vessels form side branches. The caval portions of the post-cardinals grow back into the tail as paired vessels, forming no connection with the caudal vein. In **Protopterus** there is no vertebral vein, and the subcardinals are not fused behind, while the advehent veins are connected with the caudal.

### **Pulmonary Veins:**

There may be various pairs of these. They carry blood from the lungs to the left auricle of the heart. They never empty into the sinus venosus.

## **THE LYMPHATIC SYSTEM**

In addition to the arterial and venous divisions of the circulatory system, all craniates develop **lymph-vessels** or **lymphatics**.

These consist of a network of lymph capillaries which are interwoven with, but independent of, the blood-capillaries. The lymphatic system is not closed like the blood-vascular system, for there are not only definite lymph vessels, but there are large open spaces—the **lymph-sinuses**. Then, too, there are connections by little apertures, called **stomata**, between the lymphatics and the coelom.

Lymph sinuses are found beneath the skin, as in the frog, between muscles, in the mesenteries, in the walls of the alimentary tract, around the central nervous system, and in many other parts of the body.

The lymph (which is practically the liquid part of the blood which seeps through the blood vessel walls) is gathered into these sinuses and then passes into more or less definite lymph vessels which, in turn, open into the veins (Fig. 453).

Leukocytes are added to the plasma from the various lymphatic glands (Fig. 453), such as the tonsils, thymus, and spleen.

In the lower craniates, such as the frog, lymph-hearts occur (Fig. 347). These are muscular dilations found in the course of certain vessels.

The lymph glands (Fig. 453) are made up of a network of connective tissue in which the lymph leukocytes (**lymphocytes**) are formed.

The function of lymph glands, therefore, seems to be that of destroying foreign bodies and to add white blood corpuscles to the general

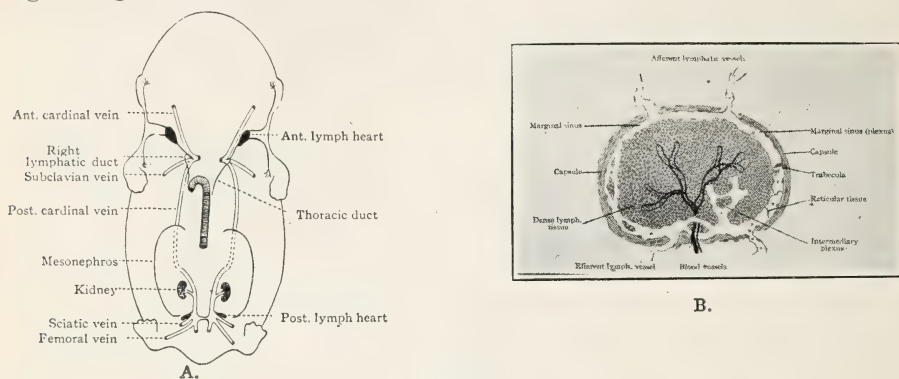


Fig. 453.

A, Diagram showing arrangement of lymphatic vessels in a 20 mm. pig embryo. (After Sabin.)

B, Diagram illustrating a stage in the development of a lymph gland. (After Stöhr.)

circulation. The lymph itself bathes all the cells of the body. There are no red blood corpuscles in lymph.

The lymphatics of the intestine are called **lacteals** and perform the important function of absorbing fats from the ingested food. These lacteals combine with the lymphatic vessels from the hind limbs and body to form a receptacle known as the **receptaculum chyli**, from which a tube (**thoracic duct**) passes cephalad to open into one of the large veins of the precaval system by a valvular opening. The thoracic duct is often double.

In mammals, the lymphatic system ramifies throughout all portions of the body. The lymphatic system is too delicate to be worked out by the ordinary laboratory dissection.

## SUMMARY OF THE CIRCULATORY SYSTEM

### AMPHIOXUS (Fig. 444)

The blood vessels are all of one kind, but due to various homologies with the more complex vessels of higher animal forms, some are called **arteries** and others **veins**.

The circulatory system consists of a ventral pulsating vessel without a specialized heart enlargement. This pulsating vessel pumps the colorless blood forward and through the branchial arches to be aerated. The blood then collects in paired dorsal aortae which unite back of the pharynx into a single dorsal aorta. Branches are sent from this dorsal aorta to the walls of the intestine where they break up into capillaries.

The blood is collected from these capillaries into a median longitudinal **sub-intestinal vein**, through which it flows forward to pass into the **hepatic portal vein** at the origin of the liver. This portal vein breaks up into capillaries within the liver, and the blood is then collected in the **hepatic vein** which extends along the dorsal portion of the digestive gland, where it turns downward and forward to join the caudal end of the ventral pulsating vessel.

The vascular system of **Amphioxus**, therefore, consists primarily of (a) a dorsal vessel represented by the paired and unpaired dorsal aortae, (b) a ventral vessel represented by the subintestinal vein and the ventral aorta, and (c) commissural vessels represented by the afferent and efferent branchial arteries and the intestinal capillaries. This is quite similar to the circulation in the earthworm except for two important differences. The blood in the ventral vessel of **Amphioxus** travels forward, that in the dorsal vessel backward (just the reverse of what occurs in the earthworm), while the ventral vessel is broken up into two parts, by the interposition in its course of the capillaries of the liver, so that all the blood from the intestine has to pass through the liver before reaching the ventral aorta. This passage of the intestinal blood through the vessels of the liver constitutes the **hepatic portal system**, which is characteristic of all vertebrates.

## FISHES

The circulation in fishes corresponds quite closely in the main to that of the chick's embryonic circulation. It is built about the gill system. The blood is pumped forward from the ventral heart through the gills, and then, as arterial blood, it is carried backward in the dorsal aorta. This scheme of circulation, wherever found, is interpreted as **primarily aquatic**.

The heart consists of four chambers: (a) **sinus venosus**, (b) **auricle**, (c) **ventricle**, and (d) **conus arteriosus**, through which blood passes in the order given. The sinus and auricle lie dorsal to the ventricle.

In the lampreys there is no portal system.

In the dogfish (Figs. 446, 449, 454), the circulation is laid out in accord with the branchial system. The blood brought to the heart by the venae cavae is pumped forward through a common ventral aorta which divides into five pairs of **afferent branchial arteries**, each of which carries blood to one set of branchiae. A corresponding **efferent branchial vessel** picks up the aerated blood from the branchiae and carries it to a dorsal aorta, through which it is distributed to all parts of the body, both anteriorly and posteriorly. The **general systemic, hepatic-portal, and renal-portal systems** return the blood to the heart along dorsal vessels called **anterior and posterior cardinal veins**.

The fish-type of circulation is built primarily along lines laid down by the branchial respiration, and the heart pumps blood forward and



**pulmonary arches.** It is of interest to note that in all lung-breathing fishes, the lungs are supplied from the branch of the sixth branchial arch. In most amphibia, a branch of the **sixth** arch becomes **cutaneous**, for the skin respiration is almost as important as the pulmonary. The heart is carried back into the trunk and consists of a sinus venosus, right and left auricle, ventricle, and conus arteriosus. The auricle has divided into a systemic half and a pulmonary half which lie in front of the ventricle. The single ventricle receives both arterial and venous blood, but there is very little mixture of the two.

The postcava is well developed. The lateral abdominal veins (also called epigastric) unite to form an anterior abdominal vein. This latter vein permits the return of blood from the hind legs to the heart either through the anterior abdominal and the hepatic portal system, or the renal portal system and the postcava.

### REPTILIA (Figs. 447, 448, 452, 455)

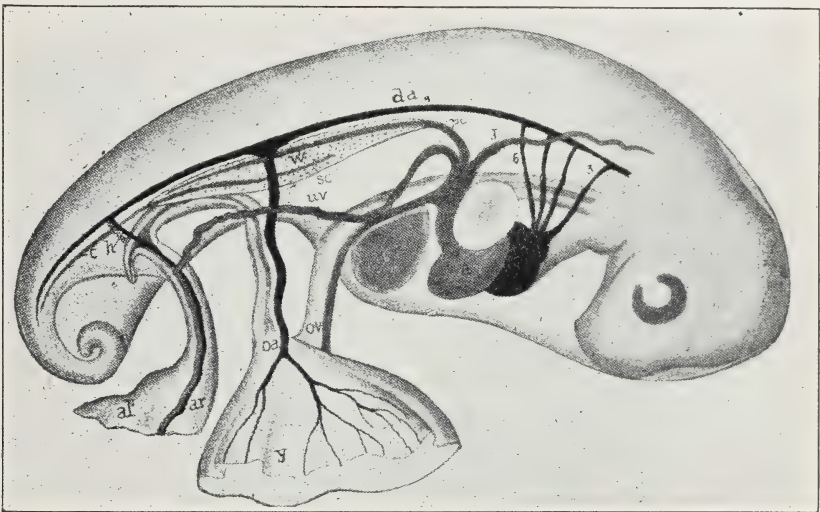


Fig. 455.

Embryonic circulation of a Snapping Turtle (*Chelydra*) to show the relations of allantois. *a*, right auricle; *al*, allantois; *av*, allantoic vessels; *c*, caudal vein; *da*, dorsal aorta; *h*, hypogastric artery; *j*, jugular; *l*, liver; *oa*, *ov*, omphalomesenteric artery and vein; *pc*, post-cardinal; *sc*, subcardinal vein; *uv*, umbilical vein; *w*, Wolffian body; *y*, yolk-sac; 3-6, aortic arches. (From Kingsley after Agassiz and Clarke.)

The heart is very broad laterally and consists of a sinus venosus (although only distinguishable in *Sphenodon* externally), two quite distinct auricles (the right receiving venous blood from the body, and the left aerated blood from the lungs), and a ventricle always more or less completely divided into right and left portions. (In the crocodile the partition is complete.)

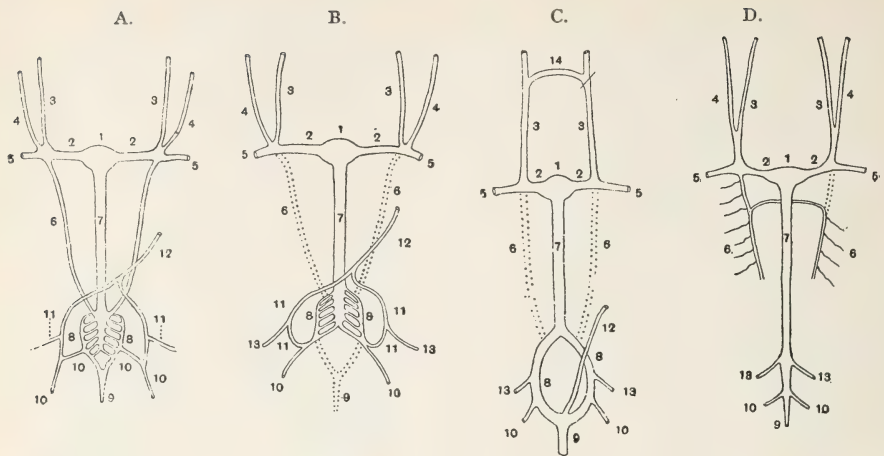


Fig. 456.

Diagrams to show arrangement of principal veins in A, *Urodele*, B, *Anura* and *Reptilia*, C, *Bird*, D, *Mammal*. 1, Sinus venosus, gradually disappearing in the higher forms; 2, Ductus Cuvieri (superior vena cava); 3, Internal jugular (anterior cardinal sinus or vein); 4, External jugular (sub-branchial); 5, Subclavian; 6, Posterior cardinal, front part (venae azygos and hemiazygos of higher forms); 7, Inferior vena cava; 8, Renal portal (hinder part of posterior cardinal); 9, Caudal; 10, Sciatic (internal iliac); 11, Femoral in A, Pelvic in B; 12, Anterior abdominal in A and B, coccygeomesenteric in C; 13, Femoral (external iliac) in B, C, and D; 14, Anastomosis of jugulars in C. (From Shipley and MacBride.)

The sinus venosus receives the venous blood from two precaval (really the Cuvierian duct) and one postcaval vein. The blood passes through the right auricle into the right half of the ventricle, after which it passes through the **pulmonary arteries to the lungs**. From the lungs it returns through the **pulmonary veins** to the left auricle and thence to the left ventricle. From here it is pumped out through the paired aortic arches to all parts of the body. There are both a renal and an hepatic portal system.

Often there is a foramen (of Panizza) connecting the right and left fourth aortic arches, so that blood can pass from one side to the other.

### BIRDS (Figs. 444, 446, 447, 448, 452)

The heart is large and has two definite auricles, two ventricles, and no distinct sinus venosus. The right auricle receives the venous blood from the general body, while the left receives the aerated blood as it is returned from the lungs. The **right aortic arch** carries all of the arterial blood to the body-system. The renal-portal system is vestigial.

### MAMMALIA

Mammals retain the **left aortic arch** and lose the right, while birds retain the right arch and lose the left. Modern reptiles show a tendency to reduce the left arch.

The valves between auricle and ventricle are tricuspid on the right

side and bicuspid (mitral) on the left. In the monotremes, however, both valves have three cusps.

The pulmonary artery and aorta have three-lobed semilunar valves.

In the monotremes, the renal portal system is better developed than in other mammals, although in all mammals it functions for a short time and disappears with the degeneration of the mesonephroi (Wolffian bodies).

A part of the capillary system of the mesonephroi enlarges during the degenerative process to form a main trunk which connects the post-cava with the caudal portions of the post-cardinal veins. It is the post-cardinals that drain the tail, iliacs, and metanephroi.

The left post-cardinal largely disappears later with the exception of that portion which connects with the suprarenal and gonad of the left side. All the blood from the posterior part of the body is, therefore, returned through the right post-cardinal and the postcava, whose origin appears to be at the union of the iliac veins.

The postcaval vein in the turtle unites with that part of the renal portal system which lies caudal to the kidneys, and the renal portal system then passes out of existence.

This can be understood the better if it is remembered that the renal portal veins are the caudal portions of the posterior cardinal veins, and that the subcardinal veins (particularly the right subcardinal) form the postcaval vein which lies between the kidneys.

In mammals, the postcaval vein is formed principally of the distal ends of the posterior cardinal veins, and of the right subcardinal of the (vitelline) hepatic veins close to, and cephalad to, the liver, as well as of the hepatic veins which lie between the liver and the hind limbs. As the postcaval vein is made up of so many different sources, there are bound to be many variations in the adult state due to more or less persistent embryonic conditions.

The more anterior portion of the post-cardinal veins loses its connection with the portion connecting with the excretory organs, and with the thoracic portion of the supracardinals, to become the **azygous** vein on the right side and the **hemiazygous** on the left. Either of these may disappear or, as in man, there may be a cross connection between these two veins. In such a case the anterior part of the hemiazygous is known as the **superior intercostal vein**.

The abdominal veins are quite important in foetal life as they bring blood from the placenta to the embryo.

In the higher vertebrates, including man, an **innominate** vein extends across from the carotid-subclavian trunk from one side to the other. All the blood is thus returned to the heart by means of the base of the right trunk, which is now called the **precava** or **vena cava anterior**.

The Cuvierian duct remains only as the **coronary sinus**.

## CHAPTER XXVI

### THE UROGENITAL SYSTEM

**A**S has already been noted, not only in the frog but in several of the type-forms studied, there is an intimate connection between the excretory and the reproductive systems. In fact, this connection is so intimate that it is impossible to take up either subject without touching upon the other. For this reason, it is customary to treat both under the head of the **Urogenital System**. The excretory organs, consisting of the paired **kidneys** or **nephridic organs and their ducts**, serve the purpose of casting out of the body the waste matter containing nitrogen, and occasionally other substances.

The **gonads** (ovaries or testes) are the reproductive glands. To any and all of these, accessory structures are frequently added. The nephridic organs proper have already been quite fully described in the frog, a review of which is essential to the understanding of that which follows.

It will be remembered that the kidneys are **parenchymatous glands**, composed of a soft, more or less spongy, tissue in which there is a profuse quantity of blood. This great quantity of blood is sent through the tiny venules which anastomose with the arterial capillaries in the **Malpighian corpuscles** (Fig. 16, Vol. I).

Some of the typical parts, which go to make up the kidneys of higher forms, are lacking in certain groups of animals. In the amniotes, nephrostomes are never formed, although they do occur in most ichthyopsida. In the pronephros, the Malpighian corpuscle is rudimentary or lacking at all stages while there is no differentiation of convoluted tubules and Henle's loop.

Professor Kingsley's excellent account of the urogenital system is followed here.

Theoretically the function of the various parts of the nephridial tubules is in outline as follows: In the primitive condition, the nitrogenous waste is elaborated in the liver, collected in the coelom and, together with the coelomic fluid, is passed outward through the nephrostomes and the tubules which act merely as ducts. "Higher in the scale the parts become more differentiated and specialized. The renal corpuscles form a filtering apparatus by which water is passed from the blood-vessels of the glomerulus into the tubules near their beginning, and this serves to carry out the urea, uric acid, etc., secreted by the glandular portions of the walls of the tubules (convoluted tubules, ascending limb of Henle's loop)."

"All three nephridia arise from the mesomeric somites or from the Woffian ridge which appears on either side of the median line where the mesomeres separate from the rest of the wall of the body cavity, the

mesomeric cells furnishing the nephrogenous tissue from which the definitive organs develop."

"Three views are held as to their relations one to another. According to one they are parts of an originally continuous excretory organ (holonephros) which extended the length of the body cavity. This has become broken up into the separate parts which differ merely in time of development and function, with minor modifications in details. A second view is that they are three separate organs, while a third regards them as superimposed structures which occasionally overlap (birds, gymnophiona) and thus are not, strictly speaking, homologous but rather homodynamous. The first view has the most in its support, but for convenience the three structures are kept distinct."

It is of considerable value to trace the successive series of these excretory structures in the different types of animals. It will be remembered that in some of the forms studied, such as the earthworm, there was an excretory organ in practically every segment of the animal's body. It will be remembered further that the so-called higher animal forms have practically every structure that the lower forms possess, **plus something additional**. This is well exemplified in the study of the nephridic organs.

The nephridic organs of the amniotes pass through a three-fold development. The first excretory organ, which grows, forms the **pronephros** or **head-kidney**; the next succeeding is known as the **mesonephros** or **Wolffian body**; while the last to form, which becomes the **permanent kidney** of the higher forms, is called the **metanephros**.

While all three are closely related both in their development and their structure, there is a difference in their origin and in some of the details.

### THE PRONEPHROS

As its name implies, the pronephros is the first of the excretory organs to appear. A review of the embryology of the excretory system must be had at this point.

As the myotome is being formed from the epimere, the dorsal end of each mesomere closes. This forms a sac which opens into the coelom. Each of these is called a **nephrotome** and lies a little behind the head. It is from these nephrotomes that the pronephros is formed. The number of pronephridic organs varies from one in the teleosts to a dozen or more in the caecilians. The usual number, however, in the higher forms is two. From the somatic walls of these nephrotomes there is an outgrowth toward the ectoderm. This forms slender pronephric tubules as in the amphibia, or solid cords which later have a lumen form within them as in elasmobranchs and amniotes. They thus all become tubules; the proximal ends of each communicates with the metacoel by way of the cavity in the nephrotome. The opening to the metacoel is called a **nephrostome** and, as already noted, there will be as many tubules and

nephrostomes as there are somites. The distal ends of the nephrotomes grow outward until they reach just below the ectoderm when they bend toward the caudal end of the body. Here the more cephalic tubules fuse with those behind and it is at this meeting place of the tube that the **pronephric duct**, sometimes called the **archinephric duct**, grows backward immediately beneath the ectoderm. This backward growth continues until the caudal end of the metacoel has been reached. It is here that the pronephric duct fuses with the caudal end of the digestive tract and empties into the cloaca, as in the frog, where it meets with the ectoderm close to the anal opening. In either case an opening then breaks through so that the contents of the duct can be expelled.

The question is often asked as to whether the ducts thus formed are of mesothelial origin or whether the ectoderm contributes a share. From present evidence it is assumed that the ectoderm has no share in their formation.

The pronephros functions for a time in embryos of some of the lower vertebrates, while in higher forms only a part remains as the **oviducts** and the **ostium tubae abdominale** of the female.

During the functional embryonic period the pronephros carries nitrogenous waste from the body-cavity. Its filtering apparatus is made up either of a separate **glomerulus** to each tubule or a group of glomeruli from the separate somites to form a **glomus**.

Neither the glomeruli nor the glomus project into Bowman's capsule, but, lie directly above the dorsal wall of the coelom between mesentery and nephrostomes, pushing the epithelium before them.

Later, both glomeruli (or glomus) and nephrostomes may become enclosed in a cavity which has become cut off from the coelom, appearing quite like a renal capsule, although the renal capsule is different in origin.

The nitrogenous fluid passes into the metacoel from where it is drawn by the cilia of the nephrostomes to pass along through the tubules.

Short segmental arteries from the dorsal aorta bring the blood to the glomeruli or glomus. After this blood has flown through the capillaries, it passes through the post-cardinal veins to the heart. The post-cardinals develop backward just as rapidly as the tubules of the pronephros grow in that direction.

In all vertebrate adults, with the possible exception of **Bdellostoma** (Fig. 366), the pronephros has been replaced by the mesonephros and later still in the amniotes by the metanephros. In the cyclostomes and a few teleosts, the pronephros, however, persists.

### THE MESONEPHROS

The mesonephros, also called the **Wolffian body**, is formed by a series of mesonephric tubules which are developed after the pronephros and its ducts are completely formed. The mesonephric tubules grow

out from the nephrotomes behind those which form the pronephros. The tubules extend toward each side of the animal until they meet and fuse with the pronephric duct. This duct is then the excretory canal for the mesonephros. The points of origin of the mesonephric tubules vary in different animals. Some lie dorsal to the pronephric tubules, while two arise from the same nephrotome one above the other. In fish and amphibians, the nephrostome consists of the opening of the nephrotome into the metacoele. As this opening, however, is closed in the amniotes even before the tubules are formed, there are no nephrostomes, and consequently there is no connection between tubules and the peritoneal cavity.

In nearly all the higher forms (in some rodents this is not true) segmental arteries from the aorta grow out to the splanchnic wall of each nephrotome to form a network of capillaries. These growths take place at a level somewhat higher than the pronephric glomeruli.

The capillaries form glomeruli which press against the wall of the nephrotome. The rest of the nephrotome closes around the pressed-in portion to form a Bowman's capsule. The capsule, together with the enclosed capillaries, is a Malpighian body.

In most ichthyopsida, the nephrostome connects the Malpighian body with the metacoele on one side, while the mesonephric tubule connects with it on the other.

The mesonephros is metameric at first. It extends over many more somites than the pronephros, reaching nearly to the posterior limits of the metacoele.

As the embryo develops, the number of tubules increases (in all vertebrates except the mxyinoids) by budding. The tubules then unite with those first formed so as to form collecting tubules from their distal portions. A separate Malpighian body is formed for each of the secondary tubules. All the tubules elongate, become convoluted, and the mesonephros ceases to be metameric.

Changes in circulation are also taking place. The veins which carry blood from the renal corpuscles extend into the region of the tubules. Each vein breaks up into a second system of capillaries which envelop the tubules before returning the blood through the post-cardinal vein. It is the subcardinal vein which brings the blood from the posterior body-region to the Wolffian body, from whence it is returned to the heart through the post-cardinals.

### THE MESONEPHRIC DUCTS

In those animals, seemingly more primitive, such as the elasmobranchs and in some of the amphibia, the pronephric duct divides longitudinally from its most caudal end forward almost to the cephalic end of the Wolffian body. This occurs at the time the mesonephros develops. There are thus two ducts formed one of which, called **Wolffian**, or **Leydig's, duct**, remains connected with the tubules of the mesonephros and

forms its excretory canal, while the other, called the **Müllerian duct**, is also quite closely related to the pronephros, but forms the oviduct in the female. In the amniotes, the pronephric duct does not divide but becomes the Wolffian duct, while the oviduct arises in another manner. (See page 390.) This same condition is found in many of the amphibians and in all of the teleosts.

### THE METANEPHROS

While the mesonephros functions in all vertebrate embryos and throughout the entire life of fish and amphibians, as well as a short time after birth in the lizards and opossum, this organ becomes replaced in the adult of all amniotes by the two metanephridic organs which form the **true kidneys**. Each of this pair of kidneys takes its origin directly behind the mesonephros of the same side, while from the caudal end of the Wolffian duct, close to its entrance into the cloaca, a tube, the **ureter**, grows forward, parallel to the parent duct, into the tissue caudal and dorsal to the mesonephros. It is supposed that this is more or less metameric although all trace of such metamerism has disappeared, the kidneys not being segmented at any stage of their development. The cephalic end of the ureter has a varying number of branches, whose tips expand to form what is called a **primary renal vesicle**. Around each primary vesicle, a group of cells develops, the aggregate of which grows into an "S" shaped tubule, one end of which connects with the primary renal vesicle, the other developing into a **glomerulus**. There are no nephrostomes. Still later these tubules multiply extensively and the blood capillary system of the glomerulus increases also.

### THE URINARY BLADDER

This reservoir for urine, also called a **urocyst**, forms toward the caudal end of the excretory ducts. There are three kinds of urocysts:

1. A bladder arising by the **fusion of the caudal ends** of the Wolffian ducts plus a portion of the digestive tract. This is the **cloaca type**. The Wolffian ducts in such cases empty into the cloaca, the cloaca then opening to the exterior.

2. The usual urinary bladder formed by a **diverticulum from the dorsal wall** of the cloaca cephalad to the openings of the Wolffian ducts. It is supposed, however, that this form may be homologous with the rectal gland of the elasmobranchs.

3. The **allantoic bladder** occurring in all higher forms as a **ventral diverticulum** from the cloaca. The entire outgrowth forms the bladder in amphibia, while **in the amniotes only the proximal portion** becomes the bladder. The distal portion is used in the embryo as a **respiratory organ**, the **allantois**. The allantois is quite extensive and forms a part of the placenta in mammals. It is either absorbed or lost at or before the time of birth.

In the higher forms in which a bladder is present, the ureters open

directly into it, the urine being conveyed to the exterior through the single tube, the **urethra**; in amphibia the urine must first pass through the cloaca before entering the bladder, as the Wolffian ducts do not directly enter the urocyst. In many birds and reptiles there is no urinary bladder at all, although these have an allantois during their embryonic development.

The nephridic tubules are quite like those studied in the earthworm. The nephrostomes open into the coelom while convoluted tubules envelop a network of capillaries. In the earthworm each tubule opens separately to the exterior in the somite behind the one in which the nephrostome lies; but, in vertebrates the whole series of tubules empty into a common duct. Much work is still needed to explain the nephridic system satisfactorily.

### THE REPRODUCTIVE ORGANS

A detailed study of the embryological beginnings and development of the reproductive organs has already been covered in that part of this book devoted to embryology. After this has been reviewed it will be understood how the germ plasm from which the gonads develop is set aside very early in the growing embryo. The gonads are not segmented, notwithstanding the fact that earlier writers have taken another view.

These sexual organs in their growth, push a layer of peritoneum before them just as do the other outgrowths in the body. Such peritoneum covering the male gonad, which serves as a support for the testes, is called a **mesorchium**, while that supporting the ovaries is known as a **mesovarium**. In all the higher forms gonads are paired. In many fishes and birds they are **unpaired**, due to a fusion of two or to a degeneration of one.

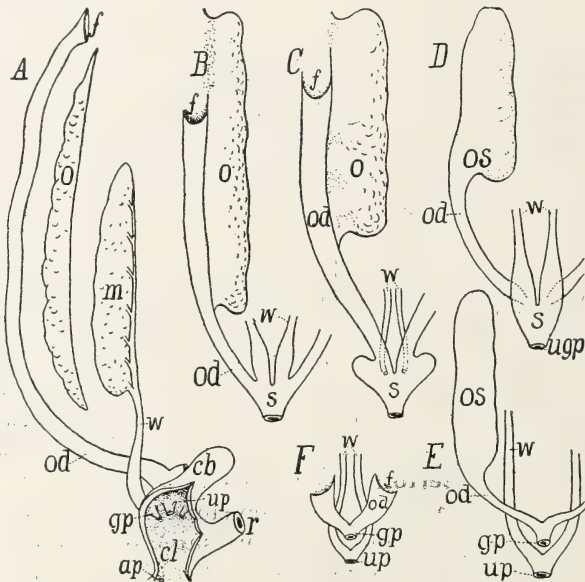
We have seen in our embryological study how the gametes are formed in the female and lie within a **Graafian follicle** which, after rupture, leaves a scar in the form of a **corpus luteum**, while in the male, instead of the primordial ova and the epithelial cells becoming separate follicles, they develop into a **cord** which later on has a lumen open through it to become the seminiferous tubule. Both epithelial cells and primordial spermatagonia may be found in the walls of this tubule. A third type, known as **Sertoli's cell**, is also found here. These latter are called **nutritive** or **nurse cells** for the developing spermatozoa. Just what function these cells have aside from this supposed nursing, is unknown. The testes remain in the position where they first appear in most vertebrates, but in nearly all the mammals they descend to assume a position outside the body cavity. They are enclosed in a special pouch called the scrotum.

### THE REPRODUCTIVE DUCTS

As fertilization is necessary in at least all the higher forms of animals, there must be some method by which the sperm or the eggs,

as well as the young in viviparous animals, may be carried to the outside of the body. The sperm-ducts of the mammal are known as **vasa deferentia**. (Fig. 457.) The egg ducts of the female are called **oviducts** (**Fallopian tubes**). The vasa deferentia are usually the Wolffian ducts, but in the female the oviducts may be **either the Müllerian ducts, or specially developed tubes, or even merely abdominal pores**. In practically all the forms we are studying, the Wolffian ducts serve as the outlet for the sperm.

At the same time that the tubules, which are to carry the sperm, are developing, there is an outgrowth of cells from the Bowman's capsules at the cephalic end of the mesonephros to form **medullary cords**. These latter continue their growth into the **genital ridge** until they connect with the **seminiferous tubules**. All of these acquire a lumen and both together form a continuous transverse tubule, known as the **vasa efferens**. (Fig. 458.) This continuous tube leads from the genital cells to the Malpighian corpuscles and thence by the mesonephric tubules to the Wolffian duct. The vasa efferentia become connected by a longitudinal canal before actually entering the Wolffian body. There is also usually a second longitudinal canal which connects them in the body of the testes. The connection of testis



I.

Fig. 457.

I. Diagrams of urogenital systems of female fishes. A, African lungfish *Protopterus*; B, African ganoid *Polypterus*; C, American garpike *Lepisosteus*; D, most teleosts; E, trout and salmon. ap, abdominal pore; cb, cloacal bladder; cl, cloaca; f, funnel of oviduct; gp, genital pore or papilla; m, mesonephros; o, ovary; od, oviduct; r, rectum; s, urogenital sinus; up, urogenital pore (papilla); ugp, urogenital pore (papilla); w, Wolffian ducts. (From Kingsley after Goodrich.)

## II.

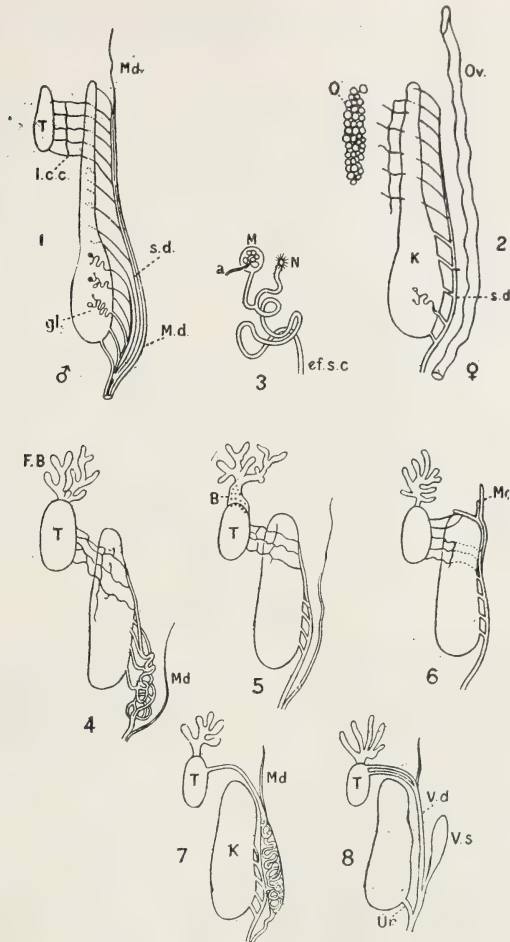


Fig. 457.

II. Diagrammatic representation of the modifications of the urogenital ducts. 1, 2, male and female Newt. 3, a tubule of the kidney. 4, Male Frog. 5, Male Toad. 6, Male *Bombinator* (European Frog). 7, Male *Discoglossus* (Fire-bellied toad). 8, Male *Alytes* (obstetrical toad). *d*, artery entering and producing a coil in the Malpighian body; *M*, Bidder's organ; *ef.s.c.*, efferent segmental canal; *F.B.*, fat-body; *gl*, glomerulus; *K*, kidney; *l.c.c.*, longitudinal collecting tubule; *M*, Malpighian body; *Md*, Müllerian duct; *N*, nephrostome; *O*, ovary; *ov*, oviduct; *s.d.*, segmental duct; *T*, testis; *Ur*, ureter; *V.d.*, vas deferens; *V.s.*, seminal vesicle. (After Gadow.)

and Wolffian body, while usually taking place at the cephalic end of the mesonephros, may, as in some of the lung fishes, take place at the caudal end.

At about this time the glomeruli of the tubules degenerate. This means that the part of the mesonephros in which these glomeruli degenerate is no longer excretory, but has become a part of the reproductive

**system.** It will be noted, then, that sperm can pass throughout the lumen of a tube the entire distance from their origin to their exit from the body.

The cephalic end of the Wolffian duct becomes purely reproductive in the male, it being considerably coiled to form the **epididymis**. (Fig. 458.) In the amniotes, where the hinder portion of the mesonphros is supplanted by the true kidney (metanephros), the whole Wolffian duct is a sperm duct (vas deferens) in the male, while in the female it largely or completely degenerates. In the amphibia and elasmobranchs the hinder end of the duct is both reproductive and excretory in the male. In the female it is purely excretory.

"In the ichthyopsida, other than elasmobranchs and amphibia, the sperm is carried to the exterior in other ways, and there is no connection of the testes with the excretory organs. In the cyclostomes the sperm escapes from the testes into the coelom and then is passed to the exterior by way of the abdominal pores which in the lampreys open into a cavity (**sinus urogenitalis**, Fig. 457) which also receives the hinder ends of the Wolffian ducts. In the myxinoids the pores are united, and they open to the exterior behind the anus and between it and the urinary openings."

## OVIDUCTS

As already stated, in many forms, the Müllerian duct is the direct result of the splitting in two of the pronephric duct which then serves as the oviduct. At its separation from the Wolffian duct the Müllerian duct opens into the coelom by means of the pronephric tubules and their nephrostomes. These then flow together and form a larger opening, called the **ostium tubae abdominale**, on each side. (Fig. 458.) In the elasmobranchs the ostia are usually united ventral to the liver. The eggs which are thrown out of the ovaries into the coelom are picked up by the somewhat trumpet shaped extensions around the ostia and carried into the oviduct. In some forms the pronephric tubules and nephrostomes take part in the formation of the ostium tubae and the beginning of the oviduct; however, as in all the higher forms, the remainder of the oviduct arises by the formation of a groove of the peritoneal membrane close beside the Wolffian duct. This becomes rolled into a tube to form the Müllerian duct. In the amniotes the anterior end of the groove does not close, but remains open as the ostium tubae. (Fig. 458.)

It is difficult to trace the successive stages from the most primitive to the most highly developed types of oviducts. Some writers regard the condition of the oviduct in the elasmobranchs as the most primitive. Some contend that we have here a homologous condition—a condition resulting from similar primitive structures; others that it is rather analogous and an example of convergent evolution in that these organs, having been used for similar functions, have come to appear somewhat alike structurally.

It can be seen how difficult valid comparisons are when we have such varying conditions in the lower, but nevertheless supposedly related forms, as this: In the cyclostomes the eggs are thrown from the ovaries

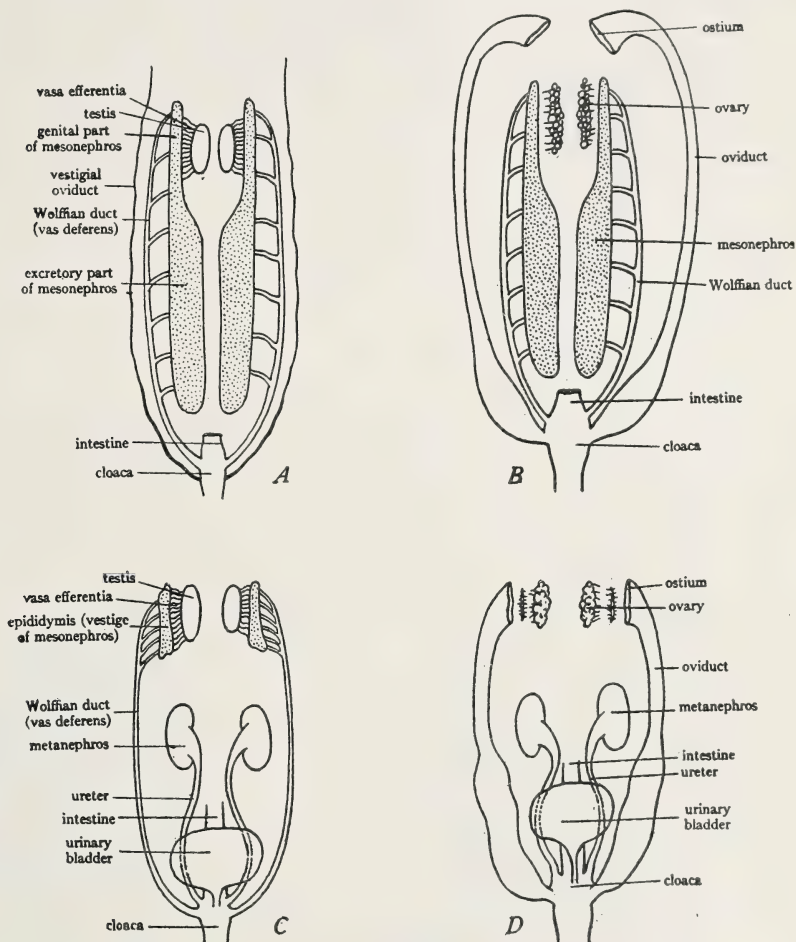


Fig. 458.

Diagrams to illustrate the urogenital system of male and female anamniotes and amniotes. *A*, male elasmobranch or amphibian; the mesonephros is differentiated into anterior genital and posterior-excretory portions; the genital part is connected with the testis by means of the vasa efferentia, which are outgrowths from the mesonephros; the mesonephric or Wolffian duct serves as both genital and excretory duct; the oviduct or Müllerian duct is vestigial. *B*, female elasmobranch or amphibian; the ovary is not connected with the mesonephros; the mesonephros and mesonephric duct serve only excretory functions; the oviduct is well developed and opens into the coelom by the ostium near the ovary. *C*, male reptile, bird, or mammal. The excretory part of the mesonephros has disappeared but the genital part persists as the epididymis (in part) which is connected as in anamniotes with the testis by means of the vasa efferentia; the Wolffian duct is purely genital and is renamed the vas deferens; the excretory function is served by the metanephroi and ureters. *D*, female reptile, bird or mammal; the mesonephros and Wolffian duct have entirely vanished; the condition of the ovary and oviduct is the same as in anamniotes; the excretory function is served by the metanephroi and ureters exactly as in the male. (From Hyman's modification of Wilder.)

directly into the coelom, being passed out through abdominal pores; in the teleosts alone there are several conditions, the ovaries of some are simple and composed of solid bands or are sac-like, having an internal lumen. In the simple forms the eggs pass into the coelom and thence to the exterior by abdominal pores or by oviducts of varying lengths. We do not know whether these ducts are true Müllerian ducts or whether they are new formations.

The sacular condition of the ovaries may come about by the free edge of the ovary bending laterally and fusing with the wall of the coelom. This forms a cavity, called the **parovarial canal**, closed in front. Or there may be a groove in the covering epithelium forming on the surface of the ovary. In this case, as it closes and sinks inward, it forms what is called an **entovarial canal**. In either case the canal may extend to the most caudal end of the body cavity and form an oviduct in this manner, or the oviduct may be formed from both kinds of canals, one in front, the other behind.

"From this it would appear that the ovary originally extended back to the hinder end of the coelom (as it does in **Cyclopterus**) or that the par- or entovarial canal had united with a Müllerian duct which has otherwise been entirely lost. The oviducts thus formed usually unite before opening to the exterior, either directly or via a urogenital sinus."

It will be remembered that there are **shell glands** (likewise called **nidamental glands**) in those animals which are oviparous, although these may appear in viviparous forms also; they are but slightly developed in these latter instances. It is interesting to note that in some species of elasmobranchs the eggs are larger than those of an ostrich. In this same type of animal the caudal or inner side of the pelvic fin is specialized for a copulatory organ as fertilization is internal in the elasmobranch. In the amphibia, there are many interesting accessory reproductive relations, as mentioned in the chapter on classification of vertebrates. The caecilians and **Amphiuma** lay their eggs in long strings in the soil and the female incubates them, although the male often takes charge of the eggs. In **Pipa**, each egg undergoes development in a pit in the skin of the back of the female, and in **Nototrema** and **Opisthodelphys** (South American tree-toads), there is a large pocket in the skin of the back, opening near the coccyx, where the eggs are carried until partially (**Nototrema**) or entirely developed. **Salamandra maculosa** and **S. atra** bring forth living young, the former possessing gills at birth, the latter in the adult form.

In the higher forms of vertebrates there is a definite single copulatory organ. Among the sauropsida **Sphenodon** alone lacks all copulatory organs, while in most birds they are incomplete. The males of crocodiles, turtles, ostriches, ducks, geese, and swans are among the very few that have a definite structure homologous to that of mammals for

this purpose. In snakes and lizards, several sacs are developed from the caudal wall of the transverse anus. They resemble appendages in the embryo and form real copulatory organs called hemipenes. They are present in both sexes though very small in the female. As growth continues, retractor muscles are developed which draw the organs back into pockets where they are retained at all times except when used for copulation. The simplest form of the copulatory organ is produced by a thickening of the ventral wall of the cloaca. There is a longitudinal groove, formed in the upper surface of this, through which the sperm may pass. It may be divided into right and left halves, the tip of which forms the glans penis. The homologous structure is the clitoris which forms in the female though all parts but the glans are lacking.

In the mammals, while there are two pronephric tubules outlined in the embryo, they never are functional and the pronephros degenerates. The mesonephros, however, is definitely used during foetal life, and in the marsupials and monotremes it even functions sometimes after birth. However, in all forms of mammals it disappears in time, with the exception of the efferent ductules of the testes and a few remnants in both sexes. The metanephros, which becomes the permanent kidney, has several lobes in the early stages. A definite lobe is formed for each end branch of the ureter so that each lobule has its own duct. This condition is retained in "adult elephants, some ungulates, carnivores and

primates, and especially in the aquatic species (whales, seals), the lobules being most numerous (200+) in some whales. In all other species the ducts fuse and the lobules unite later into a compact mass lying in the lumbar region near the last rib." These lobules are the cause of the cortex and medulla of the kidneys forming two series of interlocking pyramids. (Fig. 459).

In the early embryonic stages the gonads lie cephalad to the kidneys.

The ovaries are usually equally developed in the mammals except in the monotremes; here the left is the larger. "It is of interest that eggs—one in the *Echidna*, two in *Ornithorhynchus*—have been found only in the left oviduct." The ovaries, unlike the testes, always remain in the body, and in the monotremes retain their early position. "They are supported by the mesovaria which are attached to the median side of the double fold of the peritoneum which supports the mesonephros. When

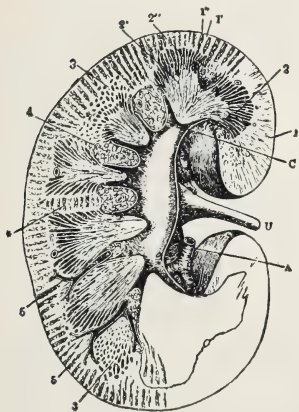


Fig. 459.

Longitudinal section through kidney. 1, cortex; 1', medullary rays; 1'', labyrinth; 2, medulla; 2', papillary portion of medulla; 2'', boundary of medulla; 3, transverse section of tubules in the boundary layer; 4, fat of renal sinus; 5, artery; transverse medullary rays; A, branch of renal artery; C, renal calyx; U, ureter. The pyramids are located between the fat portions and form the papillae. (From Hill after Tyson and Henle.)

the Wolffian body degenerates, the fold becomes the **broad ligament** while another fold continues down the Müllerian duct as the **ligament of the ovary**. In some mammals the ovaries have, in addition, a special fold of the peritoneum, which in the rats and mice encloses the ovary and the ostium tubae connected with its opening."

"The testes are relatively small and are shaped much like the ovaries and at first they are at about the same level. The outer surface is smooth, a fibrous envelope, the tunica albuginea, having developed around them, which sends trabeculae inward, dividing the seminiferous tubules into lobules. Except in the monotremes, the testes descend farther into the pelvic cavity, remaining permanently in the pelvis in many insectivores, some edentates, elephants, whales and **Hyrax**. In other groups they pass outside the pelvic cavity to be enclosed in a special sac, the scrotum. The testes are supported by a cord, the **gubernaculum**, the homologue of both ligaments of the ovary.

"The change in position of ovary and testis is accomplished in part by the unequal growth of body wall and the supporting ligaments. In the case of the male this **descent of the testes** is complicated. (Fig. 460.) In outline it is as follows: By the unequal growth of gubernaculum and body wall, the testes are drawn down into the scrotum which is a protruding part of the body wall into which a part of the coelom extends. This wall is formed in part from the genital folds which surround the genital eminence. It lies in front of the penis in the marsupials, behind it in all placental mammals. When the canal connecting the cavity of the scrotum (**bursa inguinalis**) remains open as it does in marsupials, bats, rodents, insectivores, etc., the descent is temporary, the testes being withdrawn into the peritoneal cavity at the close of the breeding season by the **cremaster muscle**, developed from the transverse abdominal muscle. In other mammals the descent is permanent, though sometimes it does not occur until the time of sexual maturity."

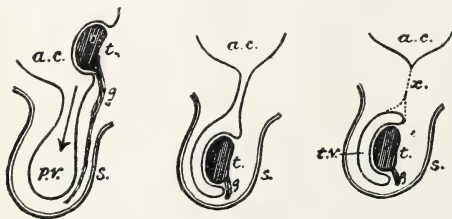


Fig. 460.

Descent of the testis *ac*, abdominal cavity; *g*, gubernaculum; *pv*, processus vaginalis; *t*, testis; *s*, scrotum; *tv*, tunica vaginalis; *x*, rudiment of processus vaginalis.

In the monotremes, the Müllerian duct is divided into a cephalic portion, known as the **Fallopian tube**, and a caudal portion, the **uterus**, although the line separating these two is not very definite. The broad trumpet-shaped end of the Fallopian tube connects with the coelom, while the tube itself secretes the albuminous

covering of the eggs. The uterus is more muscular than the Fallopian tube, and it is here that the horny shell is formed. The uterus then opens directly into the urogenital sinus to connect the cloaca with the exterior.

In other forms of mammals, the end of the Müllerian duct between the uterus and the urogenital sinus forms a vagina. In marsupials there are two vaginae and sometimes three.

When the two caudal ends of the Müllerian ducts fuse as in many placental animals, such as in rodents, two uteri are formed, each with a separate opening into the vagina. (Fig. 461.) In the carnivores and ruminants where the fusion is carried still farther back, forming in reality two uteri with only one opening, it is called a **uterus bipartitus**; where it is carried still farther, forming two horns, it is called **uterus bicornuus**. For the **uterus simplex** the fusion is entirely complete, as in all primates, the two Fallopian tubes alone remaining as evidence of its bilateral formation.

In the female, the Wolffian duct and the mesonephros are largely

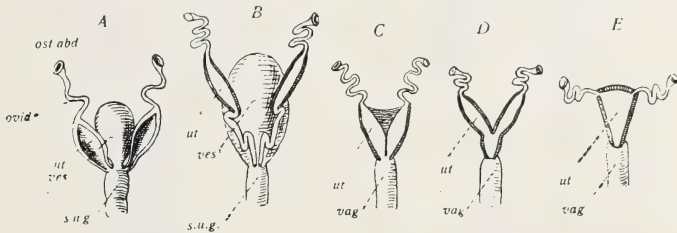


Fig. 461.

Five varying uteri. *A* Monotreme; *B*, Marsupials; *C*, duplex uterus; *D*, bicornuate uterus, and *E*, Simple uterus. *ost.abd.*, abdominal opening (ostium) into oviduct; *ovid.*, oviduct; *s.u.g.*, urogenital sinus; *ut.*, uterus; *vag.*, vagina; *ves.*, urinary bladder. Such uteri as *A* and *B* open into the urogenital sinus, while *C*, *D*, and *E*, open into the vagina. (After M. Weber.)

lost in the adult; the mesonephros forms a small collection of tubules near the anterior end of the ovary which is known as the **parovarium**. The Müllerian duct in the male is also largely lost, the lower portion sometimes persisting as a small blind tubule imbedded in the prostate gland and known as the **uterus masculinus**. (Fig. 462.)

Between the tubules in the testes there are small aggregates of cells known as **interstitial cells**, which are glands of internal secretion. In man, their products, which pass into the blood, apparently cause the assumption of the secondary male characters—growth of hair on the face, change of voice, etc.—at the time of puberty. There would also seem to be some analogous structure in the ovary governing the development of female characteristics and controlling some of the features of menstruation.

There are also a number of accessory glands (Fig. 462) connected with the genital ducts, usually better developed in the male than in the female. The more prominent ones are: the **seminal vesicles** (present in some rodents, bats, insectivores and in ungulates and primates), a pair of tubular or saccular glands opening into the vasa deferentia just before these enter into the urogenital canal; the **prostate glands** (occurring

in all placental mammals with the exception of edentates and whales), connected with the urogenital canal; and farther along the canal **Cowper's glands** are found. These occur in almost all mammals as scattered bodies or aggregated into larger masses surrounded by smooth muscle.

Considerable uncertainty exists as to the exact functions of any of these glands. The removal of the prostate and the seminal vesicle in rats prevents fertilization, while the secretion of the seminal vesicles increases the activity of the spermatozoa. It seems probable that they are of great importance in connection with fertilization. It has also been shown that in some instances the coagulation of the secretion of these glands closes the vagina after copulation and thus prevents the exit of the sperm.

In the monotremes, the cloaca serves as a general gathering place for both the products of the urogenital sinus and the excreted matter

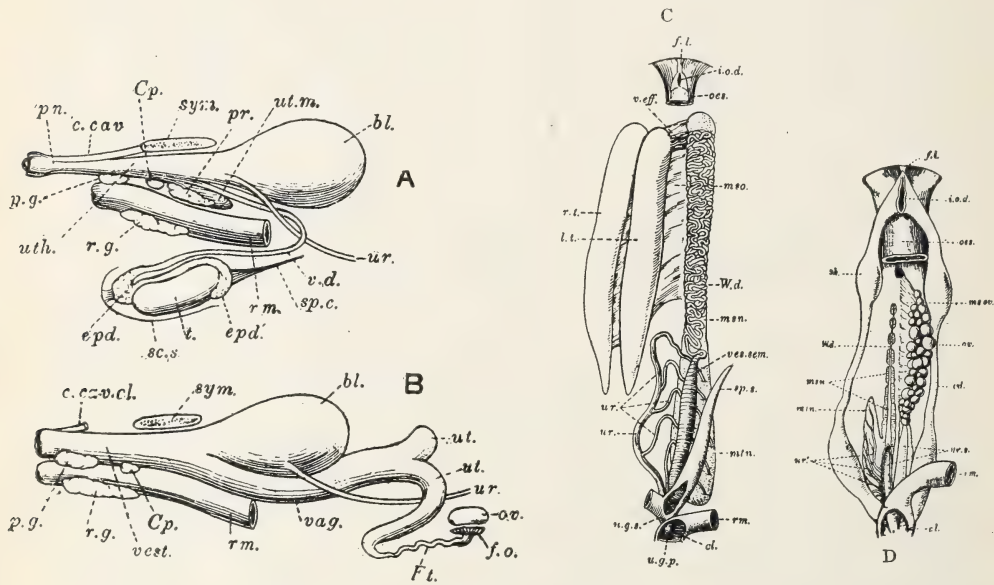


Fig. 462.

A B The reproductive organs of the rabbit. A, male; B, female. In each case the dissection is made from the left side, the animal lying on its back. *bl.*, Bladder; *c.cav.*, corpus cavernosum; *c.cav.cl.*, corpus cavernosum of the clitoris; *Cp.*, Cowper's gland; *epd.*, cauda epididymis; *epd'*, caput epididymis; *F.t.*, Fallopian tube; *f.o.*, fimbriated opening of the same; *ov.*, ovary; *p.g.*, perineal gland; *pn.*, penis; *pr.*, prostate; *r.g.*, rectal gland; *rm.*, rectum; *sc.s.*, scrotal sac; *sp.c.*, spermatic cord (cut short); *sym.*, symphysis pubis; *t.*, testis; *ur.*, ureter; *ut.*, uterus; *ut.m.*, uterus masculinus; *uth.*, urethra; *v.d.*, vas deferens; *vag.*, vagina; *vest.*, vestibule.

C, male, and D, female reproductive organs of dogfish. *cl.*, Cloaca; *f.l.*, "falciform" ligament; *i.o.d.*, rudiment of the internal opening of the oviducts; *l.t.*, left testis; *msn.*, mesonephros; *mso.*, mesorchium; *mtn.*, metanephros; *od.*, oviduct; *oes.*, oesophagus; *ov.*, ovary; *r.t.*, right testis; *rm.*, rectum; *sh.*, shell gland; *sp.s.*, sperm sac; *u.g.p.* and *v.p.*, urinogenital papilla; *u.g.s.* and *u.r.s.*, urinogenital sinus; *ur.*, ureter; *ur'*, ducts of metanephros; *v.eff.*, vasa efferentia; *ves.sem.*, vesicula seminalis; *W.d.*, Wolffian duct or vas deferens.

from the digestive canal and kidneys. This cloaca has only a single opening to the exterior and it is from this fact that the name monotreme has been taken. In all other mammals there is a definite and complete separation of the faecal and urogenital matter. This separation is brought about by a horizontal partition dividing the cloaca into a dorsal rectum and a ventral urogenital portion. This space between rectum and urogenital portion is called the **perineum**.

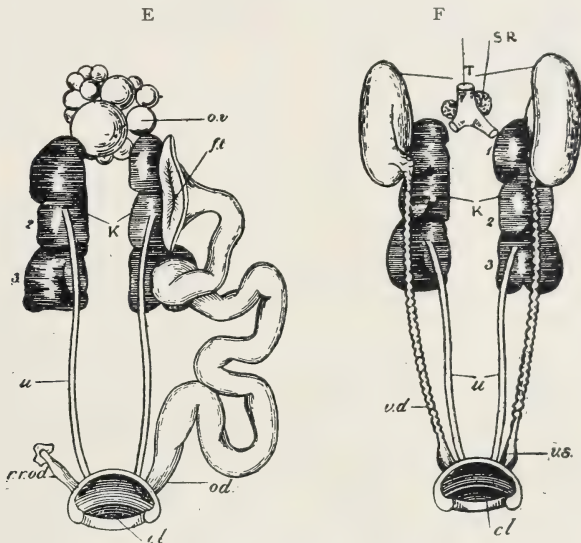


Fig. 462.

*E*, The urogenital organs of a female pigeon. *K*, kidney (metanephros) with three lobes; *u.*, ureter; *cl.*, cloaca; *ov.*, ovary; *od.*, oviduct; *f.t.*, funnel at end of oviduct; *r.r.od.*, rudimentary right oviduct.

*F*, The urogenital organs of a male pigeon. *T.*, testes; *V.*, base of inferior vena cava; *S.R.*, suprarenal glands; *K.*, kidneys with three lobes (1, 2, 3); *u.*, ureter; *v.d.*, vas deferens; *v.s.*, seminal vesicle; *cl.*, cloaca. (*A, B, C, D*, from Borradaile; *E, F*, from Thomson.)

## ORGANS OF COPULATION

In both sexes of mammals, the same anlagen of the external genitalia are found as already noted in the study of embryology. These consist of a genital prominence which is formed from the ventral or anterior wall of the cloaca. This then protrudes from the opening and, when the perineum is formed, two thickenings appear on each side, a medial genital fold and a larger and lateral ridge, which extends back nearly to the level of the anus. The genital prominence never develops much farther in the female, while the folds and ridges become the labia minora and majora. In the male, however, a groove is formed on the primitively dorsal surface of the prominence which continues into the cloaca. Then the folds grow together behind the prominence, closing the groove so as to form a tube, the **urethra**, and the prominence becomes the glans penis.

A similar growth of the genital ridges toward the median line results in the formation of the outer wall of the scrotum.

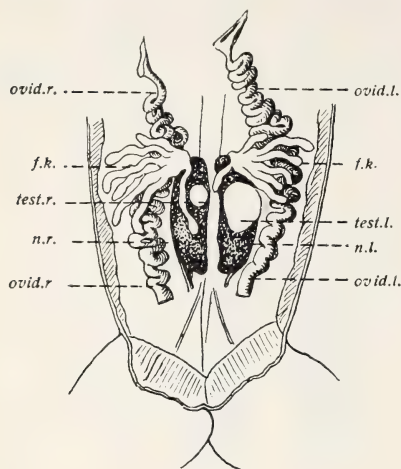


Fig. 463.

Hermaphrodite Frog. *f.k.*, fat-bodies; *n.l.* and *n.r.*, left and right mesonephroi; *ovid.l.* and *ovid.r.*, left and right oviducts; *test.l.* and *test.r.*, left and right testes. (After Mitrophanoff.)

While internal fertilization takes place in most of the higher forms of animals, there are many vertebrates, such as the cyclostomes, most fishes with the exception of the elasmobranchs, and many amphibia in which fertilization does not take place until after the eggs have passed from the body of the female. The organs by which sperm is passed to the female are formed in many ways and are not considered homologous in the different forms.

As we already know from the study of the earthworm, there are animals possessing both ovaries and testes. Such animals are commonly termed **hermaphrodites**. True hermaphrodites must have both ovaries and testes **functional**. (Fig. 463.)

It is interesting to note that, while there are occasional hermaphrodites among the lampreys, this is a rather common occurrence in the myxinoids. In these the cephalic end of the gonad is male, while the caudal end is female. However, usually, only one or the other of these functions, so that the animal is either predominantly male or female. Hermaphroditism has been found among the frogs, while in toads there is often a "**Bidder's organ**" lying directly in front of the gonads of the male but containing immature ova. (Fig. 457.) Cases of hermaphroditism, although possible, are seldom found in mammals, the so-called cases being merely arrested growth in the male, preventing the two portions of the scrotum from joining in the mid-line, or an hypertrophy of the clitoris in the female.

## ADRENAL ORGANS

Closely associated with the nephridial structures lie two small ductless glands, one connected with each renal organ in the higher forms. In the lower vertebrates each one of these is in turn composed of two structures. In the amphibia and amniotes, one portion, called the **supra-renal**, forms the medulla, while the **interrenal** forms the cortex of the mammalian adrenals. (Fig. 351.) The suprarenal portion is always connected with the sympathetic nerve ganglia, some of the cells always retaining their nervous character. Other cells, because they stain brown or yellow with chromic salts, are called **chromophile** or **phaeochrome**

cells. (Fig. 464.) These are usually quite closely related to blood vessels.

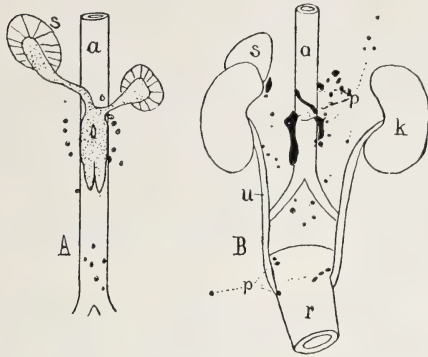


Fig. 464.

*A*, The phaeochrome system of a just-born rabbit. *B*, The same in a forty-five day girl. *a*, aorta; *k*, kidney; *p*, phaeochrome bodies; *r*, rectum; *s*, suprarenal; *u*, ureter. The connection between the bodies and the central portion of the suprarenal is shown in *A*. (From Kingsley after Kohn.)

The interrenals arise from the epithelium of the coelom. There is as yet considerable doubt as to whether they are connected with pro- or meso-nephros, or whether they are totally distinct in origin. They arise as isolated clusters, or bands, of cells near the dorsal margin of the mesentery. Sometimes they are bilaterally symmetrical, and in the lower vertebrates may extend throughout the entire length of the coelom in the early stages.

Both interrenals and suprarenals are separate in the fishes. The interrenals are the more compact of the two and lie between

the excretory organs of the two sides of the body.

The suprarenal tissue forms the medulla of the adrenals from a series of tubules through which the blood from the suprarenal artery circulates before it is carried away by the vein. The adrenals are closely associated with the Wolffian bodies in amphibia (Fig. 351), either being attached to the inner margins (urodeles), or forming yellow stripes (anura) on the ventral surface. In the reptiles they are lobulated bodies near the gonads.

It is from the medullary portion in mammals that **adrenalin**, sometimes also called **epinephrin**, is obtained. This is an **activator** or **hormone** which acts directly on the muscles and causes an increase in blood pressure.

## SUMMARY OF THE UROGENITAL SYSTEM

### Fishes (Fig. 457):

The excretory system consists of elongated bodies situated in the median dorsal part of the coelom. These bodies are composed of nephric tubules which have funnel-like nephrostomes opening into the coelom. The functional kidney is a **mesonephros**. The ovaries and testes (with the exception of the teleosts) are sac-like structures which have ducts, oviducts, and vasa efferentia developed in connection with the primitive nephridial duct, as in other groups.

In teleosts, there are no vasa efferentia or true oviducts, for the posterior ends of both testes and ovaries are continued into a duct direct; the duct from the testes unites with its fellow on the opposite side to

empty into either a urogenital sinus or directly to the outside, and the one from the ovary takes the eggs direct from the ovary before they enter the coelom as in most of the higher forms.

The eggs of different fishes range from large heavily-yolked eggs with chitinous shells, as in the modern elasmobranchs, to the small pelagic eggs of many modern teleosts. The eggs pass out through the ducts of teleosts as mentioned in the preceding paragraph or through abdominal pores as in ganoids and in some **Physostomi**.

For the most part, fish-eggs are fertilized in the open water, although there are many orders which practice internal impregnation and are viviparous.

Most of the teleosts are dioecious but some are hermaphroditic. **Serranus**, a member of the perch family, is even self-impregnating; **Chrysophrys** is successively male and female; while cod and herring often exhibit the hermaphrodite condition, though this is abnormal.

### **Dogfish (Fig. 462):**

The pronephros is never functional as an excretory organ. The nephrostomes fuse to form the **ostium tubae** in the female.

The pronephric duct splits into both a Wolffian and a Müllerian duct. The nephrostomes close in the adult. The anterior end of each mesonephros is narrowed, and, in the male, this connects with the anterior end of the Wolffian duct to form a connection with the testes. The epididymis consists of the coiled anterior end of this connection.

The Müllerian ducts become the oviducts. The oviducts of both sides connect with the coelom. The common opening thus formed is the **ostium tubae abdominale**.

The eggs leave the ovary, pass to the ostium, and are then carried backward to a shell-gland. The enlarged portion of the tube forms the uterus.

In the male, the anterior end of the mesonephros forms the epididymis while the vasa deferentia of both sides unite to form a **urogenital sinus**. There is an oval sperm-sac connected on each side. Fertilization is internal.

The suprarenals are metameric and may be imbedded in the mesonephroi.

### **Amphibia (Fig. 457):**

The pronephros functions until metamorphosis. The tubules then degenerate. In the adult frog and other tailless amphibians, the nephrostomes of the mesonephros separate from the nephridial tubules to join with branches of the renal blood vessels so that the coelom is in direct connection with the excretory system.

The Wolffian duct carries the nephridial waste and the same duct also acts as the vas deferens in the male just as it does in the dogfish.

Where these ducts enter the cloaca there is an enlargement on each to form the **seminal vesicle**.

The urinary bladder lies ventral to the cloaca. The eggs pass into the body cavity and thence into the **ostium tubae**.

Fertilization is external in the tailless amphibians, but internal in tailed amphibians. The male of the tailed amphibians secretes a substance which binds the spermatozoa into little packets called **spermato-phores**. There are various accessory reproductive relations as mentioned in the chapter on classification.

### Reptilia and Aves (Figs. 462, 465):

The kidneys are **metanephric bodies** which pass their excretion through paired ureters directly to the cloaca in the reptiles and from here into a **urinary bladder** which, in turn, empties into the **cloaca**. The pronephros never functions, and the mesonephros (always lacking nephrostomes) may function after hatching for a time in some reptiles. In the female, the mesonephros, after degenerating, is preserved as the "yellow-body." The male reproductive organs consist of a pair of testes, a pair of much coiled vasa deferentia through which the sperm passes to the grooved penis; the latter organ being attached to the front of the cloaca. The female organs consist of paired ovaries and large oviducts provided with albuminous and shell glands. The eggs when laid are covered with a tough shell; those of reptiles are usually buried in the ground. Many reptiles are, however, viviparous. The Wolffian duct is the urinary tube. The

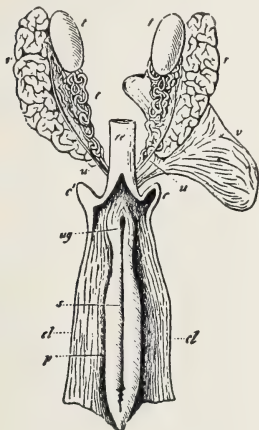


Fig. 465.

Cloaca and urogenital organs of a turtle, *Chelydra serpentina*. *c, c'*, blind sacs of cloaca; *cl*, cloaca; *e* epididymis and vas deferens; *p*, penis; *r*, kidneys; *re*, rectum; *s*, groove on penis; *t*, testis; *u*, ureter; *ug*, cloacal opening of bladder; *v*, bladder. (From Sedgwick's Zoology, after Gegenbaur.)

mesonephros functions in both sexes but later degenerates in the female. It persists in the male as the vas deferens.

In birds the left ovary alone remains functional.

### Mammalia:

Only two pronephric tubules form and these never function. The mesonephroi function in foetal life and in marsupials and monotremes for some time after birth. Nephrostomes never form except in *Echidna*. In some rodents no glomeruli occur. The kidneys are of the **metanephros type**. They are usually asymmetrical in position, one lying anterior to the other. The ureters lead directly to the urinary bladder which is formed out of the remains of the allantois.

The ovaries are never single as in birds. They are very small on account of producing minute eggs with little or no yolk. This small

size of ovaries and eggs is well fitted to the habit of uterine gestation. The paired oviducts enlarge to form paired uteri, and in some groups these unite into a single median uterus.

The testes at first lie in the body cavity, as in reptiles, and occupy positions homologous with those of the ovaries. In most mammals, with the exception of monotremes, whales, elephants, armadillos, and a few others, the testes descend into the scrotum. The penis of the male mammal is homologous with the clitoris of the female.

## CHAPTER XXVII

### THE MUSCULAR SYSTEM

**T**HE general muscular system has been discussed in considerable detail in the study of the frog, while the development of the muscles was taken up in the study of embryology.

It will be remembered that histologically there are **voluntary** and **involuntary** muscles; the former are **striated**, the latter smooth, while the heart muscles are a sort of combination of these two.

The smooth muscles have their beginnings in **mesenchyme**, and, being involuntary, are **innervated by the sympathetic nervous system**. Their action is also much slower than that of the striated muscles. They are found in the skin, in the walls of blood vessels, in the walls of the digestive canal and in the urogenital system.

The striated muscles have their origin in the walls of the coelom and are of **mesothelial origin**. They are supplied by the **motor nerves of the central nervous system**. They are all voluntary except those at the more cephalic end of the digestive tract. Striated fibers may be found in the body walls, in all organs of locomotion, in the head, in the diaphragm, and in the cephalic end of the alimentary canal.

The voluntary muscles arise from the somites (which divide into myotomes and lateral plates, after the epimeres have given rise to the sclerotomes and dermatomes).

The myotome grows downward between the hypomere and the skin to meet its fellow on the opposite side in the median ventral line. This produces a completed coat of voluntary muscles which lies beneath the skin. The muscle coat is divided into a dorsal and ventral part by the horizontal skeletogenous partition (Fig. 423) which intersects the skin at the lateral line. The dorsal muscles are called **epaxial**, and those ventral to the septum, **hypaxial**.

The muscles originating from the lateral plates in the gill-arch region, which move the gill arches, are called **visceral muscles**.

The muscles originating from the myotomes are called **parietal** or **somatic muscles**.

All muscles except the diaphragm and heart (the heart is always included under the circulatory system) are divided into three groups known as **parietal**, **visceral**, and **dermal** muscles.

From the study of embryology it will be remembered that the myotomes were cut off from the walls of the coelom, each one forming a closed sac, the inner wall called the **splanchnic layer** and the outer the **somatic layer**. The more dorsal cells of the splanchnic layer develop many nuclei which can be seen in the interior of the cell in the lower

vertebrates. They are quite close to the surface in the muscle fibers of mammals. Each myotome has its splanchnic wall converted into a muscle so that there are as many primitive muscles as there were myotomes.

The somatic wall of the myotomes does not become muscle but changes into mesenchyme from which the corium of the skin develops. Some of the mesenchyme protrudes between the various myotomes and there forms fibrous connective tissues that later become the ligaments which connect the various muscles of a side.

This primitive muscle segmentation can still be seen in the intercostal and rectus abdominis muscles.

The myotomes lie close to the level of the notochord and spinal cord, but they grow both dorsally and ventrally, working their way between the skin and the walls of the coelom to become an actual part of the somatopleure.

Ventrally, the muscles from both sides grow toward each other and, practically, meet at the mid-ventral line. The direct mid-ventral line, which is filled with connective tissues, is known as the *linea alba*.

In the fishes, the trunk and tail muscles are arranged in myomeres which take a ziz-zag course. (Fig. 401.) The muscles are divided horizontally into dorsal and ventral portions (Fig. 423), the **epaxial** and **hypaxial muscles**, a line of division which follows more or less closely the lateral line. The plates of muscle do not retain their flat ends in the adult, but one end becomes conical and fits into a corresponding hollow in the next plate. In the tail of the amphibia, epaxial and hypaxial muscles are clearly recognizable, but farther forward the hypaxials are greatly reduced, and in the amniotes, the reduction is carried so far that the epaxial muscles, greatly modified, can only be recognized in the cervical and pelvic regions, the "tender-loin" being epaxial.

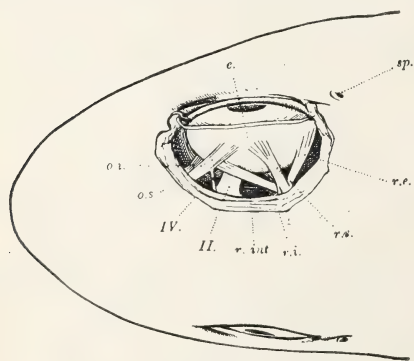


Fig. 466.

The head of a dogfish, seen from above with the right orbit opened. *e.*, eyeball; *o.i.*, *o.s.*, inferior and superior oblique muscles; *r.e.*, *r.int.*, *r.s.*, external, inferior, internal, and superior recti muscles; *s.p.*, spiracle; *II.*, optic nerve; *IV.*, fourth nerve. (From Borradaile.)

The developmental conditions are more complicated in the head than in the trunk. In the head region of fish and birds, ten coelomic pouches develop, while in amniotes the number is apparently twelve. These are known by number, with the exception of the most anterior which was not known when the numbers were applied and is called **A**. These coelomic or **head cavities** differ from the myotomes farther back by having no undivided portion

of the coelom below corresponding to the hypomeral zone. This difference is possibly due to the existence of visceral clefts in this region.

Four of these cavities lie in front of the ear of which **A** disappears completely, its cells joining the mesenchyme. The other three give rise to the "eye muscles" which move the eyeball. (Fig. 466.) In general, 1, which lies in front of the mouth, gives rise to four muscles, the **inferior oblique** and three of the **rectus muscles**; 2, which lies in the region of the jaws, forms the **superior oblique muscles**; while 3, in the hyoid region, develops the **lateral (external) rectus** (in some animals also a **retractor bulbi**). The origin of these muscles explains the distribution of the eye-muscle-nerves, as each nerve supplies only the derivatives of a single myotome. Several of the other myotomes disappear in development, but the posterior becomes the so-called **hypoglossal musculature**.

We have been describing only the origin of the **contractile tissue** of the muscles. There is also a **connective tissue** to be considered.

Mesenchyme cells invade the muscle fibers to form envelopes (**perimysium**) which bind the fibers into bundles (**fasciculi**); these in turn, are united by other envelopes called **fascia**. These connective-tissue envelopes continue beyond where the contractile tissue leaves off to form the **cords**, or **tendons**, by which the muscle is attached. The more fixed point of attachment is called the **origin**, the less fixed the **insertion**. Tendons may be of any shape; such as long and slender, so as to allow the muscle to lie in or near the trunk, the part to be moved being in the appendage; or they may form broad flat sheets (**aponeuroses**). These latter may occur not only at the ends but in the middle of a muscle.

Sometimes parts of tendons ossify, as in the patella or in the "drum-stick" of the turkey. Such small rounded ossifications of this kind are **sesamoid bones**.

In a few cases, as for example, around the eye and mouth of mammals, the parietal muscles are **without attachment**. Here they form rings which are used to diminish the size of an opening (**sphincter muscles**).

Muscles vary considerably as to shape, size, number of "heads" or points of origin, and numbers of contractile portions.

Muscles are usually arranged in **antagonistic groups** so that any given action may likewise be reversed. We thus have flexors to bend a limb and extensors to straighten it; elevators to close the jaw, depressors to open it, etc.

It is rather difficult to trace exact homologies. The test usually considered best is to **trace the nerve supply**, for every muscle derived from a given myotome is innervated by branches of the nerve which also originally connected with that segment. A further test is the origin and insertion. The **action** of a muscle is of little value in a test for homologies.

A difficulty in the drawing of conclusions from specimens before one, comes from the fact that a muscle may split into various layers either longitudinally or transversely, and some even, though entirely different in origin, may fuse together, while others, either in part or in whole, may degenerate and disappear entirely. Should one take **nerve supply** as a guide, as is usually done, it will be seen that the facial muscles, especially those of the higher mammals, have certainly wandered a long way from their embryologic origin.

The names and location of muscles of the frog should be thoroughly reviewed at this point.

In the higher vertebrates the **anterior spinalis** differs from the frog by being divided into several **rectus capitis** muscles which connect the first vertebra with the skull.

The **longissimus dorsi** group lie on each side of the vertebral spines in the angle between spinous and transverse processes and extends from the pelvis to the head. This group is made up of a **longissimus dorsi proper** in the lumbar region, an **ileo-costalis** (inserted on the dorsal part of the ribs), and a **longissimus capitis** along the side of the neck to the temporal region of the skull.

The muscles of the appendages are divided into **intrinsic** and **extrinsic** groups. The former have their origin in or on the appendicular skeleton itself; the latter have their origin on the trunk or axial skeleton and their insertion on the girdle or base of the limb. Intrinsic muscles, therefore, move parts of the limb; extrinsic move the limb as a whole. Muscles are often divided according to their action as already seen. **Protractors** draw a member forward; **retractors** pull it back against the body; **levators** lift it, and **depressors** pull it down; **flexors** bend a limb or its parts; **extensors** straighten it and **rotators** turn it upon its axis.

Some of the more prominent muscles are as follows:

**Levators:**

- trapezius (for fore limb).
- levator scapulae (for fore limb).

**Depressors:**

- pectoralis (for fore limb).
- serratus anterior (for fore limb).

**Protractors:**

- pectineus (for hind limb).
- adductors (for hind limb).
- sternocleidomastoid (for fore limb).
- levator scapulae anterior (for fore limb).

**Retractors:**

- pyriformis (for hind limb).
- pectoralis minor (for fore limb).
- latissimus dorsi (for fore limb).

The pubofemoralis draws the hind limb toward the mid-line while the gluteus muscle acts as a retractor and elevator.

### THE VISCERAL MUSCLES

As already stated, the gill-bearing vertebrates develop a special system of muscles in connection with the visceral arches which are used

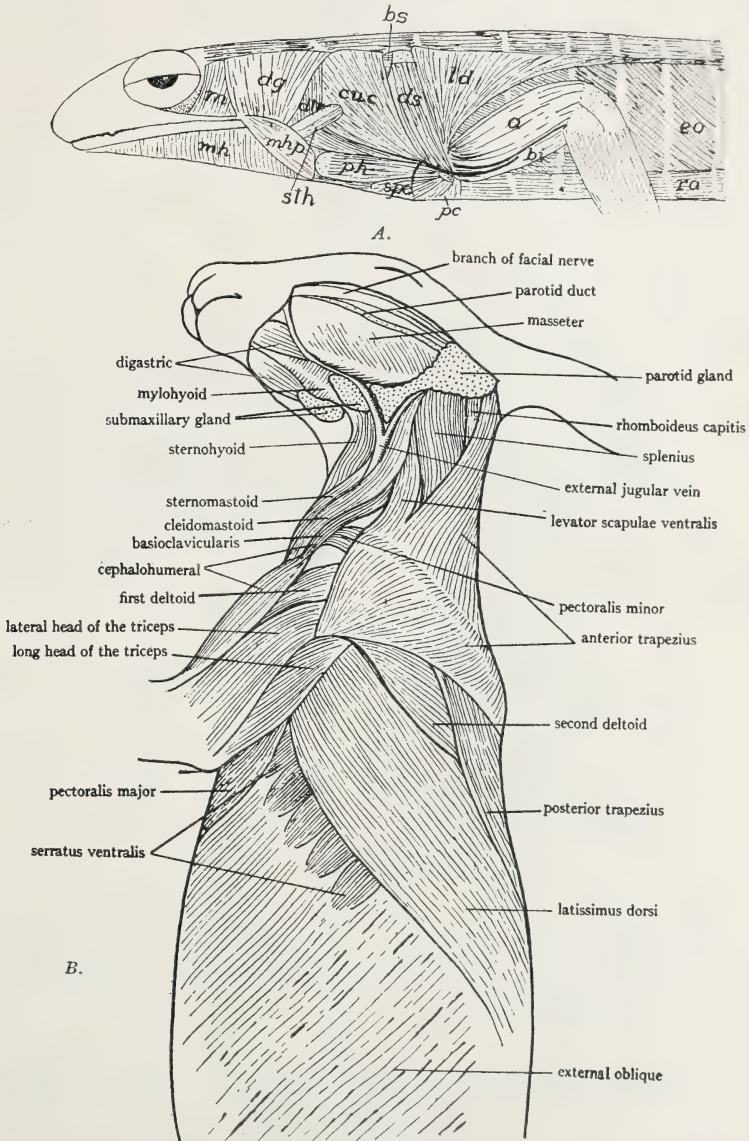


Fig. 467.

A, Superficial muscles of the cephalic part of the tailed amphibian *Salamandra maculata*. a, anconeus; bi, humero-brachialis inferior (biceps); be, levator

for the purpose of opening and closing the clefts and also the mouth. In the higher forms many of these muscles have disappeared although some do retain their connection with the hyoid.

Visceral muscles are often divided into two sets according to their

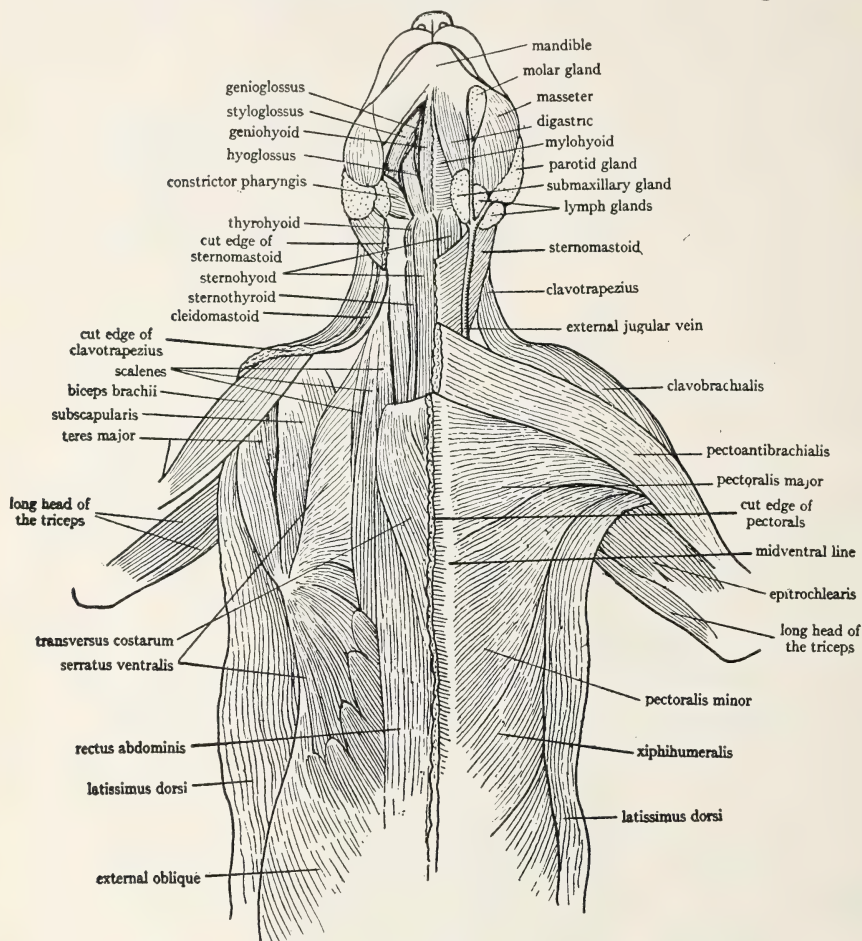


Fig. 468.

Ventral view of the anterior part of a cat to show the muscles. All dermal muscles have been removed. Superficial muscles on the right side, deeper layer of muscles on the left side, after removal of the pectoral muscles, sternomastoid, mylohyoid, and digastric. The nerves and blood vessels which cross the axilla have been omitted. The epitrochlearis is also called extensor antibrachii. (From Hyman's "A Laboratory Manual for Comparative Vertebrate Anatomy," by permission of the Chicago University Press.)

scapulae; *cuc*, cularis; *dtr*, dorso-trachealis; *dg*, digastric; *ds*, dorsalis scapulae; *eo*, external oblique; *ld*, latissimus dorsi; *m*, petro-tympano-maxillaris (masseter); *mh*, mylohyoid; *mh.p*, mylohyoid posterior; *pc*, pectoralis; *ph*, procoraco-humeralis; *ra*, rectus abdominis; *spc*, supracoracoid; *sth*, sternohyoid. (From Kingsley after Fürbringer.)

B, Lateral view of the anterior part of the rabbit to show the muscles. The head is turned slightly so as to give a ventral view of the throat. All dermal muscles have been removed. (From Hyman's "A Laboratory Manual for Comparative Vertebrate Anatomy," by permission of the University of Chicago Press.)

derivation, as some develop from muscles which originally ran in a transverse (circular) and others from muscles which ran in a longitudinal direction.

The **epibranchial** muscles, the **sub-spinals** and **interbasales** (which lie in the dorsal part of the branchial region), and the **coraco-arcuales** (in the ventral or **hypobranchial** half) are derived from the circular group. The most anterior of this circular group (Figs. 467, 468) are those which open (**digastric** or **depressor mandibulae**) or close (**adductors**) the mouth, and the **mylohyoid** which extends between the two rami of the lower jaw. There are usually several adductors, known as **masseter**, **temporalis**, or **pterygoideus**, named after the parts of the skull which serve as their origin.

The longitudinal muscles are largely confined to small slips which pass from one arch to the next. These muscles undergo considerable variation in amphibians. In the amniotes there is also much variation, but some of them are reduced on account of the loss of branchial respiration with a consequent degeneration of the parts connected with it. The most noticeable visceral muscles, therefore, in the higher groups are those connected with the opening and closing of the mouth.

Up to this point all muscles mentioned have had a direct connection with the skeletal system. With an increasing degree of development there develops a dermal musculature. Here the muscles are inserted directly in the skin although they were derived from skeletal muscles. Primitive conditions of this kind are found in reptiles and birds and serve to move scales, scutes, and feathers. This musculature attains its highest development in many of the four-footed animals, who use it to twitch

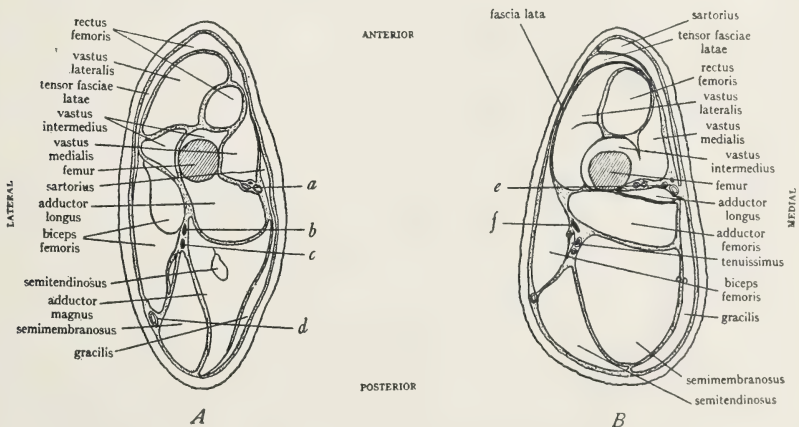


Fig. 469.

Cross-sections through the thigh of *A*, rabbit, and *B*, cat, to show the location of the muscles. Black spots are nerves, small circles, blood vessels. *a*, greater saphenous nerve, artery, and vein; *b*, peroneal nerve; *c*, tibial nerve; *d*, sciatic vein; *e*, femoral nerve, artery, and vein; *f*, sciatic nerve. (From Hyman after Bensley.)

the skin when insects attack them. In the primates, the **platysma myoides** in the neck and head is the only muscle of the kind. It is innervated by a facial nerve which in its primitive condition came from the hyoid region. The platysma divides to give rise to such muscles as the **orbiculares**, which close the lips and eyelids, and the muscles by which one lifts the lips, nose and lids, and by which some are able to move the ears.

## CHAPTER XXVIII

### THE NERVOUS SYSTEM

**I**T WILL be remembered that the nervous system begins its existence in the embryonic state by the ectoderm of the gastrula becoming flat on the dorsal surface of the embryo. This flat portion, called the **neural plate**, extends practically the entire length of the embryo. It is slightly broader at the head end than at the caudal end. The two edges of the neural plate become raised slightly and finally meet in the mid-line of the dorsal surface to form a tube. The closing of the tube begins at the head end and gradually extends backward until the tube has become completely closed. (Fig. 262.)

The neural plate, consisting of ectoderm, folding as it does, causes the interior lining of the tube to be ectoderm. This is a fact of considerable value in understanding various structures, such as the development of the eye. It is also well to remember here that the various **sense organs**, or special organs of sense, as they are often called, have to do with such things as touch, sound, taste and light, whose stimuli come first to the exterior part of the body. In the lower animal forms, such as the earthworms, there are no definite eyes, and yet, light rays, when thrown upon any part of the earthworm's body, cause it to move out of such light, showing that the animal is sensitive to these light rays even though no organ has developed by which any one particular spot is specialized to receive more impressions than another part.

Now, just as the complete digestive tract develops from a straight tube by inpushings and outpushings, so the greater portion of the nervous system has developed in a similar manner from the single nerve tube which has just been discussed.

One of the explanations given as to why the nervous system develops in the way it does from the ectoderm and on the dorsal surface of the embryo, is that remote ancestors of the vertebrates may have spent their years upon the ocean-bottom, causing the ventral surface of the body to lie in contact with the ground substance and thus serve as a protection from attack, while the upper part of the body came in contact with substances and animals inimical to it. These vertebrate ancestors thus needed a sense-perception-organ for protective and nutritive purposes. Interesting as this may be, it must be admitted that one of the great difficulties with which biologists have had to deal is the fact that, in the invertebrates, the nervous system lies upon the ventral surface. It is only in the higher forms that it lies upon the dorsal side. Several ingenious explanations have been attempted to account for all this but

none is satisfactory. Students should appreciate the fact that the complicated nervous system which controls every movement of the body is one of the most highly elaborate **protective systems** we could possibly possess.

The brain itself, the head-end of the nervous system, is enclosed in a remarkable bony case, while the spinal cord (the continuation of the brain, caudad), is encased within the slightly movable but nevertheless well fitted vertebrae that make up the spinal column. The brain and spinal cord combined are called the **central nervous system**; this to distinguish it from the **peripheral nervous system** which consists of all those nerves arising **from** the brain and spinal cord.

As the central nervous system is composed of an infolding of the outer portion of the body, the ectoderm thus infolded into the central portion of the neural tube, becomes the **sensitive part** of the central nervous system. This **sensitive surface lines the lumen** of the neural tube, and while this condition remains in all higher forms including man, it will be seen in the study of the brain that larger or smaller masses of gray matter **may migrate** to various parts of the brain.

It will be readily understood that a nervous system of this kind, which is well protected by a bony covering, has many advantages over mere external tactile-sense spots, such as the earthworm possesses; still, to be of any value whatever, any inner sensory portion must **retain its connection with the outer portion of the body**. It is such connections which, when they have definite cells and processes that unite with the central nervous system and are grouped together, become **special sense organs**. Such nerve fibers, together with their cells, are known as **sensory nerves**. Sensory nerves must, therefore, carry impulses **from outer portions** to innermost regions, or in other words, from the external portions of the body **to the central nervous system**.

The purpose of the nervous system is primarily to inform the animal of the conditions, good and bad, in the environment, to correlate this information, and to regulate the motion so that advantage may be had of this knowledge. In those forms of animals which are segmented, that is, in which metameres appear, especially when this metamerism is in the mesothelium from which the myotomes develop into muscles, there are usually one or more pairs of **motor nerves** going to these segments because each muscle must have its own nerve supply. The motor nerves carry impulses **from the central nervous system to the muscle or organ** in which they are placed.

The close association of sensory and motor nerves in the trunk region of vertebrates has not been satisfactorily explained. In **Amphioxus** the two kinds of nerves are independent of each other throughout their course which tends to show that the vertebrate condition is not primitive.

# THE SPINAL CORD

After the neural tube has formed by a joining in the dorsal mid-line of the two folds of the neural plate, the cells on each side of the neural tube proliferate very rapidly while those of the roof and floor do not. This causes an outgrowth of the two sides so that a **fissure** (Fig. 470) or

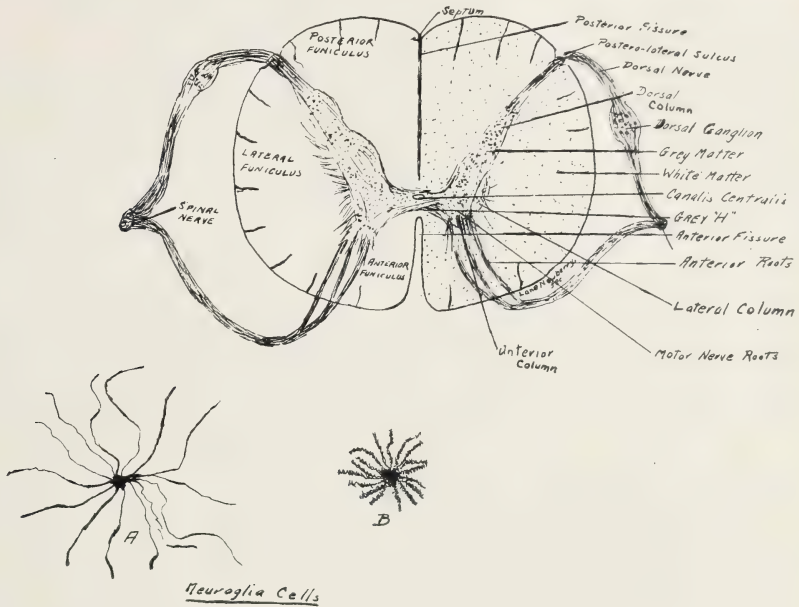


Fig. 470.

Cross-section of spinal cord. *A*, "spider" cells; *B*, "mossy" cells.

groove is formed on the ventral surface, running the whole length of the cord. In fact, the cells on each side have already begun to proliferate before the closing of the tube. There is an ingrowth of connective tissue and blood vessels on the dorsal mid-line which forms a **posterior** or **dorsal septum** dividing the dorsal part of the cord into halves. The entire lining of the central canal, composed of epithelial cells, is known as **ependyma** and, while no definite nervous cells can be seen, it is sensory and remains sensory throughout its entire career.

The remaining cells on each side develop into two kinds of cells, one called **neuroglia** or simply "**glia**" cells, which are used to support the true nerve cells; the others form **neuroblasts** which develop true nervous tissue. This latter type of cell must develop a fiber in order to connect with other cells and with other portions of the body. These are formed by a **cytoplasmic** outgrowth from the neuroblast itself. Such processes may be several feet in length or very short. Some of the little fibers produced in this way may extend out from the cord as individual nerves,

while others run longitudinally within the cord. Others run on the outside of the cord longitudinally. Those which run along the outer portion of the cord are often called the marginal layer because they form a sort of envelope of fibers for the neural cord itself. These fibers are **medulated** or covered with a white substance, and this white envelope is called the **white matter** of the cord. That portion which lies further toward the lumen and is composed largely of **cell bodies**, constitutes the **gray matter**.

In cross-sections of the spinal cord of a higher vertebrate there will be seen a portion looking something like the capital letter "H" with a central canal in the middle of the cross-bar. The entire substance, which looks like the letter "H," is the gray matter of the cord. The dorsal upright bars of the "H" form the **posterior columns**, while the ventral uprights form the **anterior columns** of the cord. Immediately lateral to the cross-bar on each side of the cord there is another column known as the **lateral column**. The lateral column differs to a considerable extent, not only in its relation but also in its function, from the dorsal and ventral column. This H-shaped gray matter really divides the white matter into **three longitudinal tracts** called **funiculi**, formerly also called columns. They are known as the **dorsal**, **ventral**, and **lateral funiculi**.

It will be remembered that the white matter is composed of longitudinal fibers. It is these longitudinal fibers which make up the various funiculi which connect the different parts of the central nervous system with each other. It is important to remember that these fibers are not all alike, but that those in the **dorsal funiculus** carry impulses **toward** the brain and are, therefore, called **ascending tracts**; while the ventral funiculus is known as the **descending tract** in that it carries fibers from the brain downward. The lateral funiculi have fibers of both kinds and carry impulses in both directions.

The fibers in each of the funiculi are again grouped into smaller bundles or **fasciculi**, each with its own name. Some of the fibers coming from the brain are distributed at different levels along the cord, while others, going to the brain, are added to the funiculi at different places. The size of the funiculi thus decreases with the distance from the brain. Some of the bundles may disappear in the more distal parts of the cord.

The spinal cord is approximately cylindrical in the higher animal forms, but in the lower it is flattened dorsoventrally, the flattening being greatest in the cyclostomes. In the lower groups there is also a difference in the shape of the gray matter, the H shape being less distinct.

The cord tapers quite regularly in fishes, from the brain to the posterior end, but when legs have developed with an increase of musculature, the spinal cord becomes enlarged in the regions where the nerves for the limbs are given off. Casts of the spinal canal in certain

fossil reptiles indicate that there was an accumulation of nervous matter near the hind legs which exceeded the brain in size.

The nerves leave the spinal cord at nearly right angles to its axis when development begins. Then there occurs an inequality in growth, the body increasing more in length than does the cord. As a result the more caudal nerves pursue a very oblique course, and in the hinder part of the spinal canal of the higher vertebrates they form a bundle of parallel nerves, the **cauda equina** (horse-tail). Often, too, another result of the unequal growth may be the drawing out of the hinder end of the cord into a slender, non-nervous thread, the **filum terminale** (Fig. 17).

### **Flexures** (Fig. 288).

In the early stages of development, it will be remembered, the head end of the developing spinal cord bends forward at almost right angles to the main axis, and this first bend is called the **primary flexure**. The second bending occurs at the most caudal end of the medulla oblongata and is called the **nuchal flexure**; it bends in the same direction as does the first or primary. The third bend is at a level with the cerebellum and is known as the **pontal flexure**; it bends in the opposite direction of the other two, thus drawing back the fore part of the entire brain to lie on top of the more rearward portion.

The three flexures just mentioned remain throughout adult life in all mammals, but even where one or more of the flexures appear in the embryonic state in vertebrates lower than mammals, it is seldom that more than one or two remain. In reptiles and birds, the nuchal and pontal flexures are weakly developed and entirely obliterated in the adult.

### **Neuromeres** (Fig. 278).

Many interesting theories have been advanced in times past as to whether or not skull and brain portion of animals were merely a continued segmented portion of the spinal column and cord. There has never been any satisfactory solution of the problem. This much we know: during its development the brain does show some traces of segmentation in a linear arrangement. These segments are called **neuromeres**, of which eight are well defined. Five lie in front of the ear, one corresponds to the ear in position, and two lie behind the ear.

It is from the first of these segments (though some insist there are two here) that the fore-brain arises, as well as the parts which in turn arise from it. The second becomes the mid-brain. The third lies in the region of the cerebellum. The fourth and fifth lie in the region of the more cephalic portion of the medulla oblongata where the trigeminal and facial nerves arise. From the sixth, the glossopharyngeal nerve arises, while the vagus is directly connected with the remaining two.

## Meninges.

In examining any brain, one finds, after the bony parts of the skull have been carefully removed, a connective tissue envelope lying close to the bone. This is called the **endorhachis**; it is really the periosteum or perichondrium of the bony parts and not a true envelope of the brain.

In the ascending groups of vertebrates we find a more complex arrangement of brain and spinal-cord-envelopes. It must be understood that what is here said of the brain-coverings proper, must also be said of the entire spinal cord.

In the fishes there is but a single covering envelope called the **meninx primitiva**. The blood vessels are carried within this meninx. There is an open space between this meninx and the endorhachis, called the **perimeningeal space**, filled, as are all such spaces, with the **cerebro-spinal fluid**. Tiny strands of tissue pass between the two connective tissue layers.

In the urodeles, and from there on upward in the various phyla, the meninx has two layers, namely, the **pia mater**, which bears the blood supply and lies close to the neural cord, and the **dura spinalis** or **dura mater**. A space between these two layers is called the **subdural space**, while the perimeningeal space is then called **peridural**.

In mammals, the outermost layer of the pia mater again separates from the pia proper, becoming a delicate **arachnoid layer**, and the space thus formed is called the **subarachnoid space**.

In man and some of the higher groups of animals, the dura spinalis unites with the endorhachis, obliterating the subdural space, and this united sheet of covering is called the **dura mater**. This dura mater forms two strong folds in the mammals, and to a small extent in birds, and presses longitudinally into the longitudinal fissures separating the two hemispheres of the brain. It is then known as the **falx cerebri**. The other fold presses transversely between cerebrum and cerebellum, forming the **tentorium**. Sometimes these folds even ossify and unite with the skull.

## THE BRAIN

The forepart of the spinal cord becomes constricted in two places transversely, forming three divisions, each hollow in the center (Fig. 288).

Starting with the cephalic end (Fig. 471), the first compartment thus formed is known as the **fore-brain** or **prosencephalon**. The central portion forms the **mid-brain** or **mesencephalon**, while the portion extending caudally is called the **hind-brain** or **rhombencephalon**.

Cyclostomes are the only vertebrates whose brains remain in this simple three-chambered state. In all other forms there are many modifications of the primitive brain, though no matter how many modifica-

tions there may be, they all form as ingrowths or outgrowths of this primary type.

The prosencephalon divides into an **end-brain**, or **telencephalon**, consisting of the **cerebral hemispheres**, and the **twixt-brain**, or **diencephalon**, consisting of the **thalamus** and the **hypothalamus**. Each of these in turn again divides, forming the parts enumerated in the accompanying table. (Pages 418, 419.)

The mesencephalon divides into **four lobes** (in mammals these are called **corpora quadrigemina** but in lower forms of vertebrates, where these bodies have not again divided transversely, they are known as the **corpora bigemina** or optic lobes), and the **cerebral peduncles**.

The rhombencephalon is made up of the **isthmus rhombencephali** (consisting of the **superior cerebellar peduncles**, the **anterior medullary velum**, the **trigonum lemnisci**, and the **crura cerebri**, the isthmus itself connecting mesencephalon and rhombencephalon), the **metencephalon** (consisting of **cerebellum** and **pons**), and the **myelencephalon** or **medulla oblongata**.

## THE CEREBRUM

The prosencephalon and the mesencephalon together are often called the **cerebrum**.

The greater part of the telencephalon is made up of the two **hemispheres** which are divided by a **longitudinal fissure**. This fissure is not well marked in fishes, but is very distinct in other groups of animals. The **lateral ventricles** are contained one in each hemisphere, while a part of the third ventricle (commonly called the **foramen of Monro**), (Fig. 303), lies between the two. The **corpus striatum** is a **ganglion mass** lying upon the floor of the lateral ventricle, while the **cortex** of the hemispheres is called the **pallium**.<sup>1</sup> The substance of the hemispheres varies to a considerable extent in the different types of animals. In fact, in the fishes it is practically all **pallium**, for there is merely a thin non-nervous covering to the ventricles. In reptiles and birds the **gray matter** (nerve cells) is to be found on the **ventricular surface**, while the outer surface is composed of **white matter** (fibers). In the reptiles there is the beginning of a second layer of cells a little distance from the ventricular surface. In birds this is still further increased, while in mammals there is a complete layer called the **cerebral cortex** over almost the entire surface of the hemisphere.

As the brain grows in a bony case, it follows that, as soon as the brain has grown longitudinally the full length of this case, it must bend in the various directions the case lays down for it. Therefore, in the mammals, the posterior end of the hemisphere grows dorsally and downward, and then forward again until that portion of the hemisphere, which

<sup>1</sup>The cortex merely means an outer portion, and, in the brain, is usually composed of gray matter, while the pallium is merely the outermost covering of the hemispheres, whether composed of gray matter or not.

was originally most posterior, has now grown forward until it reaches, or at least touches, the olfactory region. The part growing downward and then forward grows over a part of the side-wall of the hemispheres which portions of the side-wall thus form a little island in the depths of the longitudinal fissure. This island is called the **insula** (of Reil).

The bending itself of the downward and forward growing parts has caused a deep transverse fissure in each hemisphere known as the **lateral cerebral fissure** or **fissure of Sylvius**.

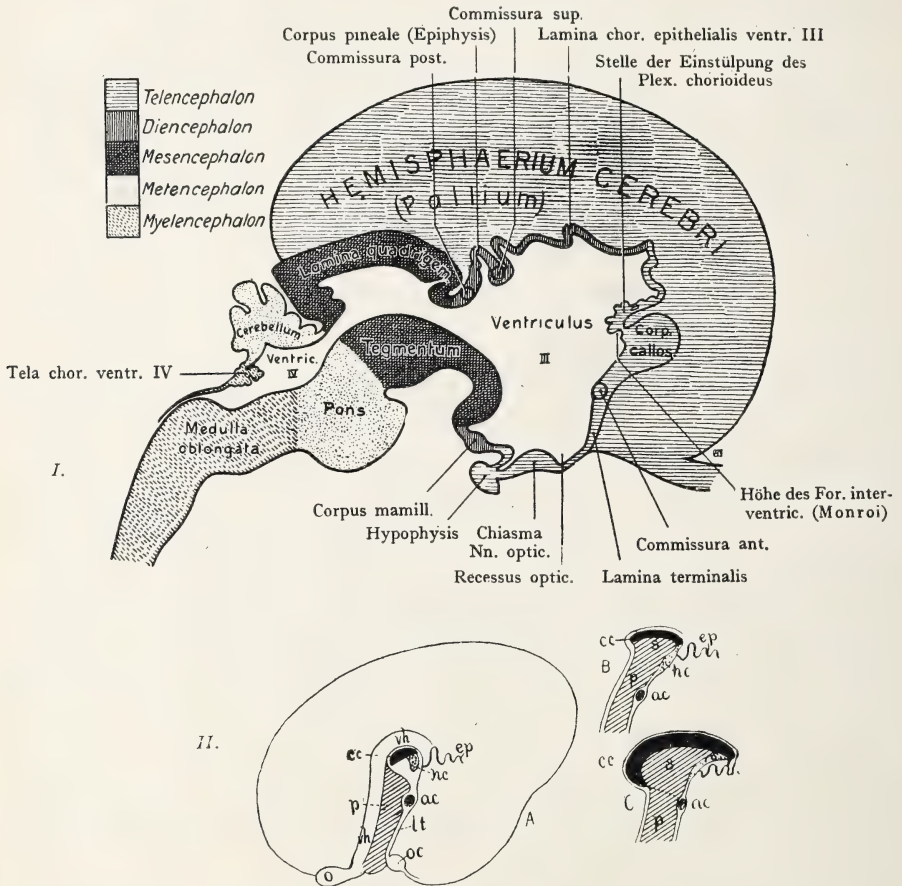


Fig. 471.

I, Schematic median section of brain of a four month human foetus to show the various changes caused by the developing hemisphere. (From Corning after Burckhardt.)

II, Diagram of the development of the corpus callosum and septum pellucidum in man. A shows the hemisphere in outline. ac, anterior commissure; cc, corpus callosum; ep, epithelial roof of the third ventricle; hc, hippocampal commissure; lt, lamina terminalis; o, olfactory lobe; oc, optic chiasma; p, paraterminal body; s, septum pellucidum; vh, vestigial precallosal and supracallosal hippocampus. (From Kingsley after G. Elliott Smith.)

All higher forms of mammals have the brain substance thrown into many folds or **convolutions** known as **gyri** (Fig. 473).

The deeper grooves separating the gyri are called **fissures**, while the lesser grooves are known as **sulci**. This folding permits a great amount of cortex, or gray matter, to be provided for; for, it will be noted that not only do the **tops** of each convolution form cortex, but also the **entire sides of every sulcus**.

The hemispheres are divided into various lobes: **frontal**, **parietal**, **temporal** and **occipital**. The two hemispheres are connected by various **commissures** which must be studied in the actual brain and compared with the diagram.

Following are the chief commissures (Fig. 471):

**Anterior commissure**, in all vertebrates.

**Pallial commissure**, dorsal to the anterior. This appears in vertebrates from the amphibians upward.

**Corpus callosum** (Fig. 471), and

**Hippocampal commissure**. These last two are a variation in the higher mammals of the pallial commissures in the lower. The corpus callosum is developed to a greater extent in man than in other animals (Fig. 472). This is explained by the fact that in no other animal does mentality reach so high a state of development as in man, and, because the cerebral hemispheres are the seat of mentality, it follows that much greater connection between the cortex of the two hemispheres is needed in man than in other animals. There is a thin translucent membrane between the body of the corpus callosum and the **fornix**, known as the **septum pellucidum**, which leaves a slight cavity between the two septa of each side. Formerly this cavity was called the **fifth ventricle**. It has no connection whatever with any of the true ventricles.

Two tracts of nervous matter run back on the medial side of either hemisphere, from the olfactory lobe to the hinder end of the cerebrum. One of these is the **hippocampus**, which passes dorsad, and the other is the olfactory tract, which goes ventral to the foramen of Monro. These two and the associated olfactory substances make up practically all of the so-called **archipallium** in the lower vertebrates, for in these the whole cerebrum really is accessory to the sense of smell. In mammals and possibly as low as the reptiles, a part has been added to receive impressions from other somatic senses. This is the **neopallium** which has grown out lateral to the hippocampus and is especially large in the higher mammals. In man it forms by far the greater part of the cerebrum. Its great development forces the olfactory parts to the medial and lower surfaces so that they are exposed to view only by dissection. A part of the original hippocampus is then vestigial.

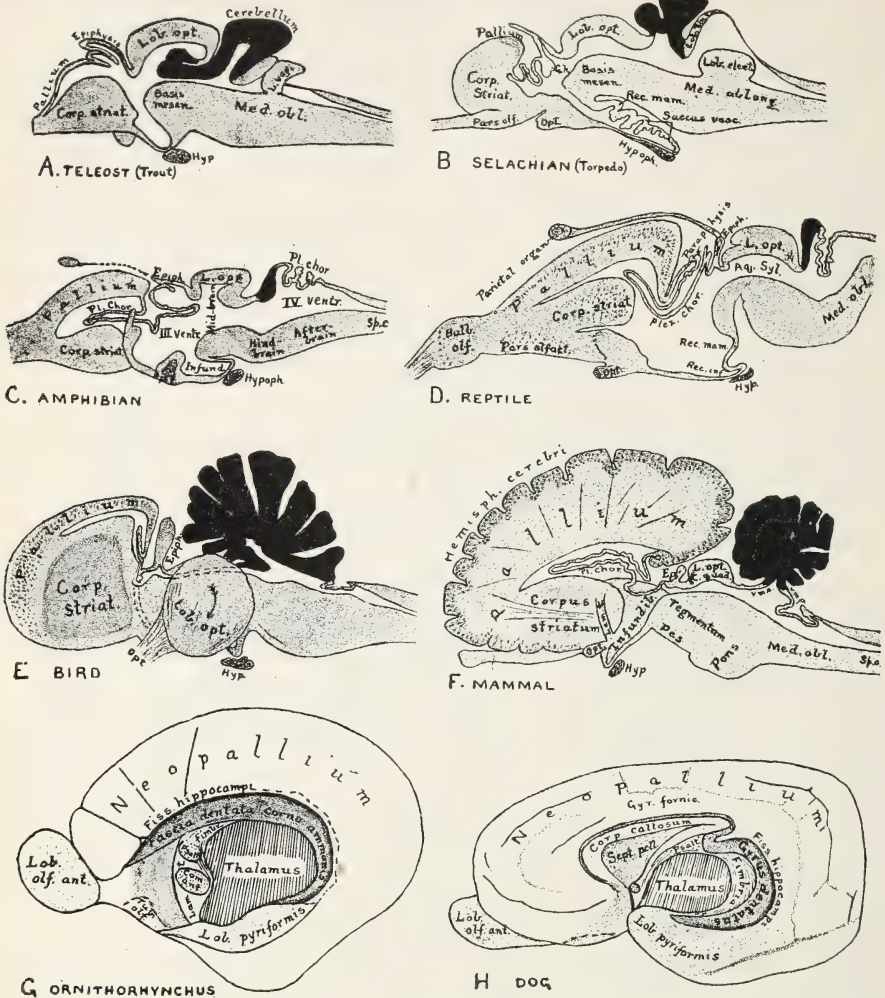


Fig. 472.

Comparison of Various Types of Brains. A-F (Edinger) are sagittal sections showing structures lying in the median line and also paired structures (e.g., pallium) lying to one side of the median line. The cerebellum is black. It is doubtful whether the membranous roof in A indicated as pallium is strictly homologous with that structure in other forms. In B, Pallium indicates prepallial structures, *Aq. Syl.*, Aquæductus Sylvii; *Basis mesen.*, basis mesencephali; *Bulb. olf.*, bulbus olfactorius; *Corp. striat.*, corpus striatum; *Epiph.*, epiphysis; *G.h.*, ganglion habenule; *Hyp.*, hypophysis; *Infund.*, infundibulum; *Lam.t.*, lamina terminalis; *Lob. elect.*, lobus electricus; *L.vagi*, lobus vagi; *L.opt.*, mid-brain roof; *Med.obl.*, medulla oblongata; *Opt.*, optic nerve; *Pl.chor.*, plexus chorioideus; *Rec.inf.*, recessus infundibuli; *Rec.mam.*, recessus mammillaris; *Saccus vas.*, saccus vasculosus; *Sp.c.*, spinal cord; *vent.*, ventricle; *v.m.a.*, velum medullare anterius; *v.m.p.*, velum medullare posterius. G and H show the mesial surface of the cerebral hemispheres in a low (G) and high (H) Mammal. G, (Elliott Smith, Edinger, slightly modified.) The exposed gray matter of the olfactory regions is shaded, the darker shade indicating the archipallium (preterminal area and hippocampal formation), the lighter shade indicating the rhinencephalon, which consists of the anterior and the posterior (principally pyriform) olfactory lobes, and a central region made up of the hippocampus and the following gyri: fornicatus, dentatus, uncinatus, introlimbicus, fasciolaris, and Andrae Retzii.

"Beginning in the amphibia and reappearing in the reptiles is a tract of fibers on either side, which connects the posterior part of the cerebrum (where the hippocampus ends) with the hypothalamus. In the mammals, by the flexure of the cerebrum, this same band of fibers, here called the **fornix**, is obliged to take a circuitous course. Starting at the hippocampus on the medial side of the temporal lobe, the fornix runs up, then forward, below the corpus callosum, and then down, in front of the interventricular foramen to end in a protuberance, the **corpus mamillare**, on the floor of the hypothalamic region."

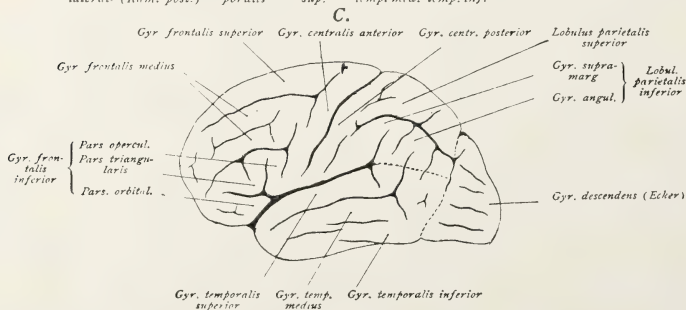
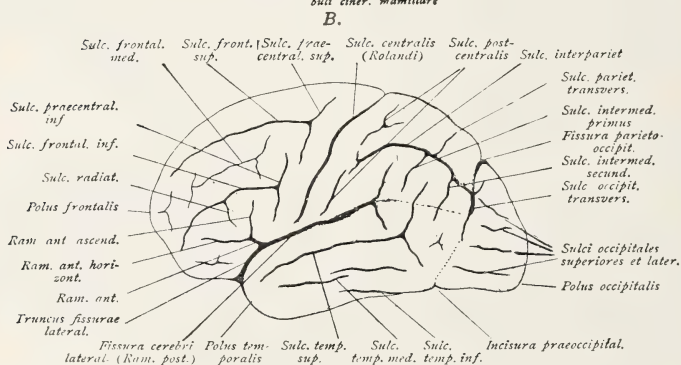
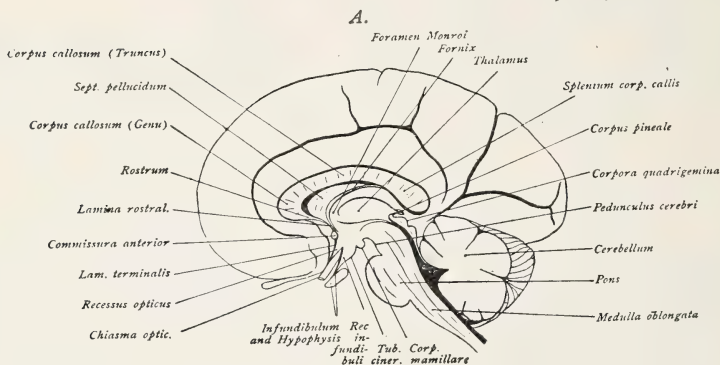
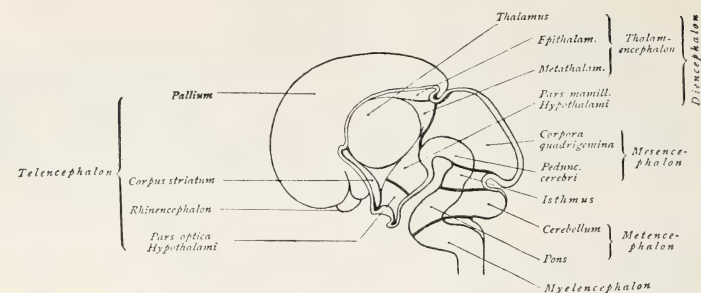
Headward, on the dorsal side, the walls become somewhat thickened, bulging out into a pair of prominences known as the **optic lobes**, or **corpora bigemina**, in the lower forms of animals, while in the mammals there are two such pairs of lobes which are, therefore, called **corpora quadrigemina** (Fig. 473). The roof of this region remains comparatively thin, but the floor becomes somewhat thicker and forms the **cerebral peduncle**. Connecting the mid-brain with the hind-brain is a short constricted area known as the **isthmus**. From here running caudad along each lateral wall there is often a groove (seldom, if ever, seen in the adult) called the **limiting sulcus** or the **sulcus of Monro**. This naturally divides the brain and spinal cord from here to the tail-end into a dorsal and a ventral half, a fact that is of considerable importance, because the entire **dorsal area is sensory**, while the **ventral is motor in character**. Further, in the study of the central nervous system's development it is the dorsal portion in which most of the changes come, comparatively few developing on the ventral side.

The hind-brain is again divided. The part lying cephalad develops into the **cerebellum** or balancing brain (organ of coördination), while the caudal end tapers rather gradually and is known as the **myelencephalon** or **medulla oblongata**. The cavity in the hind-brain, most of which is located within the medulla, is known as the **fourth ventricle**, while the small lumen which connects the third and fourth ventricle is called the **aqueductus cerebri** or the **aqueduct of Sylvius** (Fig. 282).

It will, therefore, be noticed that from the earlier three compartments of the head end of the brain and spinal cord there have developed five brain divisions with four ventricles. All the ventricles form a continuous open space throughout the entire central nervous system.

The roof plate in the region of the cerebellum, which originally was quite thick, forces the most cephalic portion of the two dorsal zones far apart, so that they then become quite thin and broad, whereas the floor plate becomes greatly thickened and constitutes the **pyramids** which pass in front into the cerebral peduncles.

A comprehensive study of the brain is a tedious and difficult task and requires a very thorough going over, and a remembering of the main points in the histology, general anatomy, and physiology of the frog. And the task is made the more difficult because all the early studies



D.

Fig. 473.

A, Diagram to show development of five secondary brain vesicles. (After His.)  
 B, Median sagittal section through brain of man. C and D, dorso-lateral cerebral surfaces. C to show fissures and sulci, and D to show gyri. (After Villiger.)

were made upon the human brain before our improved stains made it possible to understand the finer structure of nerve cells and fibers. The result is that the names of the various parts of the brain have been derived from fanciful resemblances, often very confusing.

We shall attempt to study the entire central nervous system in terms of **function** rather than in terms of **structure**, and the latter only in its development, as then, and then only, are we able to place a valid interpretation upon our findings.

Following are several terms without which no progress in this study can be made:

A **center** is any group of nerve-cells which performs a single function. (This does not imply, however, that **all** of this particular function is located in this one center alone. There may be several, or many, performing similar functions.)

It is these centers which form a sort of switchboard for the redistribution of various nervous impulses.

**Afferent fibers** are those which conduct toward the centers.

**Efferent fibers** are those which conduct away from a center.

Peripheral nerves (those running from and toward the central system) are naturally **mixed nerves** in that they carry both afferent and efferent fibers.

**Inhibitory fibers** are those which check an action.

**White matter** (substantia alba) is that portion of nerve fibers covered with white myelin sheaths.

**Gray matter** (substantia grisea) is that portion which consists of a mass of nerve-cell-bodies uncovered with myelin sheaths.

**Brain nuclei** are the gray centers **within** the brain, which are divided in turn into:

**Primary centers** which are those directly connected with the peripheral nerves, either as **terminal nuclei** of afferent

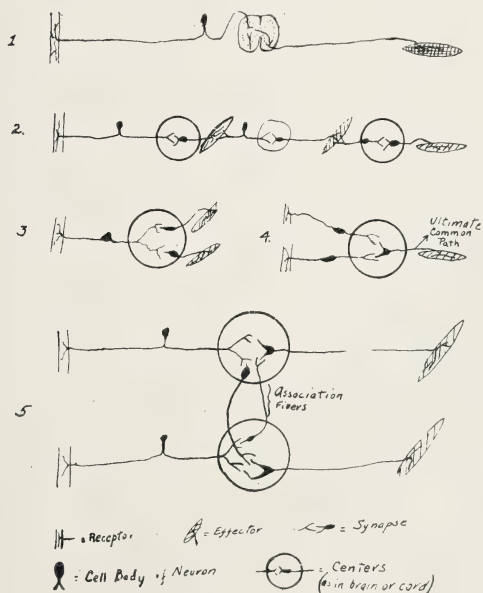


Fig. 474.  
Five types of reflex arcs.

fibers or as **nuclei of origin** of efferent fibers, and

**Correlation centers** are those in which the impulse received is redistributed after meeting with other impulses at a common center.

# BRAIN TABLE

CEREBRUM	Prosencephalon (Fore-Brain)	Telencephalon (End-Brain) Contains Lateral Ventricles.	Hemisphere	Pallium (Cortex)	This includes the lobes (frontal, parietal, temporal, and occipital); the insula, the gyri, the fissures and the sulci.
	Mesencephalon (Mid-Brain) Contains Cerebral or Sylvian Aqueduct.	Diencephalon (Inter-Brain) Contains Third Ventricle.	Hypothalamus	Stem of End-Brain	<p> <i>Peripheral Region</i> (Anterior and posterior olfactory lobes).  <i>Central Region</i> (The Hippocampus and the following gyri: fornix, catus, dentatus, uncinatus, intralimbicus, fasciolaris, and Andrae Retzi).         </p> <p>           { Nucleus caudatus.            Nucleus lentiformis.         </p> <p>           Corpus Striatum            Claustrum.            Nucleus amygdalae.            Lamina terminalis.            Optic recess.         </p>
					<p>           Optic chiasma and tract.            Tuberculum with infundibulum and hypophysis.            Mammillary bodies.         </p> <p>           Thalamus (Anterior, medial and lateral nuclei.)            Metathalamus (Geniculate bodies).            Epithalamus (Habenular region, pineal body and posterior commissure).         </p>
			Pedunculi cerebri		(Connecting the optic thalamus by a mass of fibers to the central part of the brain-stem.) The peduncles are divided into a ventral segment, the <i>base</i> and a dorsal area, called the <i>tegmentum</i> . A grayish-black substance, the <i>substantia nigra</i> , separates the

or

Corpora quadrigemina  
in mammals.  
(Corpora bigemina  
in Lower Vertebrates.)

(The anterior pair of elevations are called the *anterior* or *superior colliculi*, the posterior ones being known as *posterior* or *inferior colliculi*. The colliculi extend laterad forming an arm and called respectively the *brachium quadrigeminum superior* and *inferior*.)

The *superior cerebellar peduncles* or *crura cerebelli ad cerebrum*. (Two flattened cylindrical columns extending from cerebellum to the quadrigeminal plate.)

Isthmus  
rhombencephali

*Velum medullare anterius*. (A thin medullary sheet stretching between the superior cerebellar peduncles.)

*Trigonum lemnisci*. (A grayish triangular field.)

Cerebellum

Medial portion (known as the worm).

Lateral portions (known as cerebellar hemispheres).

Metencephalon

There are three lobes in each hemisphere corresponding to definite segments in the worm. (Lobus *superior*, *posterior* and *inferior*.)

Rhombencephalon  
(Hind-Brain)  
Contains  
Fourth Ventricle.

(The ventral side forms the *brachium pontis* or *middle cerebellar peduncle* connecting with the cerebellum dorsad. The brachium is made up of three *fasciculi*: superior, inferior and medius.)

Pons

Myelencephalon  
(Medulla oblongata.)

Ventral side (Pyramids and Olives).  
Dorsal side (Rhomboidal fossa).

Figure 474 shows the five ways in which impulses are and may be distributed.

**Ganglia** are those centers similar to brain nuclei, which lie **outside** the brain; some books still use this term interchangeably with **brain nuclei**.

**Brain stem** (also called **segmental apparatus**, because it is supposed that the primitive type of brain consisted of a mere tube of nerve-cells with which the peripheral nerves were connected, a pair passing from each segment as in the spinal cord of the higher forms) is that portion of the cephalic end of the central nervous system upon which the enormous cerebral and cerebellar hemispheres develop in all higher forms. These latter are then called the **suprasegmental apparatus**.

**Cerebrum** consists of fore-brain and mid-brain, the most cephalic part of which develops into the cerebral hemispheres which are again divided as seen in the table.

The **pallium** in the highest animal forms is the **cerebral cortex** or mantle (Fig. 472), but in the lower forms such as the fish, in which the entire hemispheres are a part of the olfactory apparatus, the pallium consists of the olfactory apparatus and the two tracts of nervous matter connecting the olfactory lobe with the hinder portion of the cerebrum. One of these tracts, the **hippocampus**, passes dorsal, and the other, the **olfactory tract**, passes ventral to the foramen of Monro. They lie on the medial side of each hemisphere.

**Archipallium** is the word now used for the pallium in the lower vertebrates where this mantle is concerned practically only with the olfactory apparatus.

**Neopallium** has, therefore, come into existence as a term to designate the pallium of the vertebrates whose brain is not governed entirely by its olfactory apparatus, but where impulses from the general somatic senses may be adjusted and be redistributed in a great correlation region—the **cerebral cortex**. In the table, the pallium corresponds to this neopallium which has grown out lateral to the hippocampus.

**Rhinencephalon** (nose-brain). The entire olfactory apparatus divides into peripheral and central regions as shown in the table.

**Corpus Striatum** (Figs. 472, 473). This is the name given to the entire mass of large nerve cells which connect the brain-stem with the cerebral hemispheres. It is also called the **basal ganglion**. It will be noted that the corpus striatum thus forms the main portion of the stem of the end brain. It is called striated because it consists of masses of gray matter separated by sheets of white matter, thus producing striations.

In the lower forms of vertebrates (Fig. 473), some have this body fairly well developed even though there be no cortex, while in reptiles and birds, in which there is a small amount of cortex, it is quite highly

developed. In these animals, the corpus striatum seems to be a reflex center of a higher order than the thalamus.

There is doubt as to the exact function of the corpus striatum. Ramon y Cajal thinks that, in mammals at least, this body functions as a reinforcement center of the descending motor impulses coming from the cortex, as these fibers give off collateral branches when passing through the corpus striatum, while the striatum itself sends important descending tracts into the thalamus and cerebral peduncle.

The white matter consists of fibers that pass between the cortex and deep parts of the brain-stem, which have no functional connection with the striatum itself. These are called **projection-fibers**, and are partly ascending and descending fibers which pass between the thalamus and the cortex, and partly descending motor projection-fibers of the cortico-spinal or pyramidal tract, cortico-bulbar tract, and cortico-pontine tracts.

The gray matter of the corpus striatum forms the two nuclei named after their respective shapes, the **caudate** and the **lentiform nucleus** (Fig. 475). Most of the projection-fibers pass between these two nuclei in a wide band of white matter which is called the **internal capsule**. These same fibers radiating from the internal capsule toward the capsule are called the **corona radiata**.

The **external capsule** is formed of a thinner sheet of fibers external to the lentiform nucleus.

Many cases of apoplexies and other cerebral diseases cause hemorrhage and other injuries in the internal capsule, there destroying some of the fibers; therefore, the study of the exact arrangement of sensory and motor projection fibers within the internal capsule is of great clinical importance.

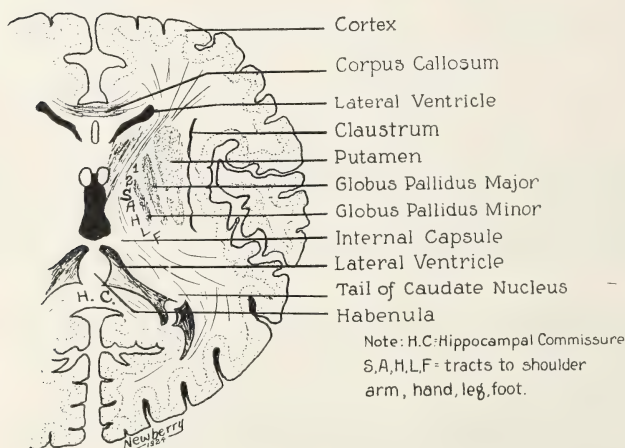
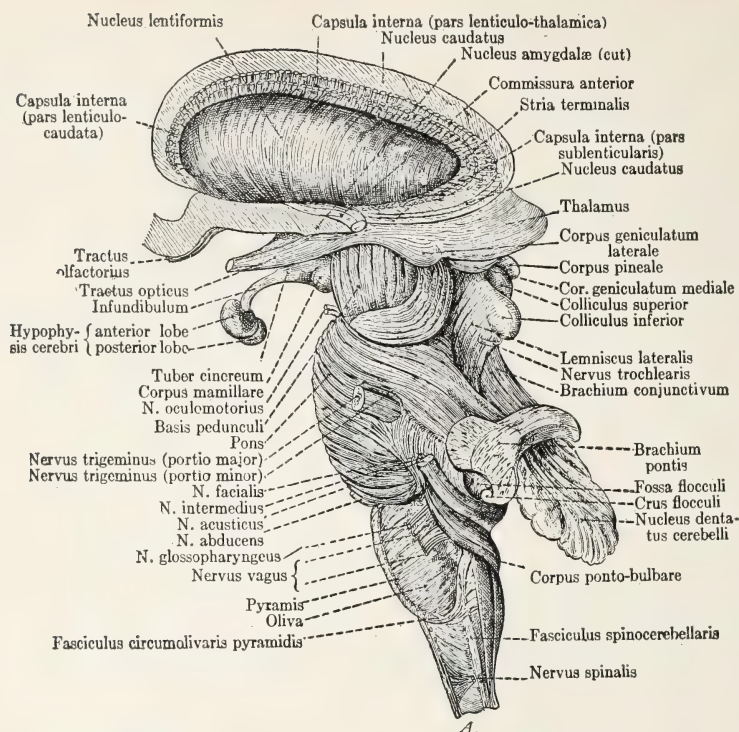
**Clastrum** is the name given to the thin band of gray matter lying between the external capsule and the cortex of the insula (Fig. 475, B).

**Nucleus amygdalae** is a small mass of sub-cortical gray matter under the tip of the temporal lobe. It forms part of the **nucleus olfactorius lateralis**.

**Thalamus** (Fig. 475). The middle and larger subdivision of the diencephalon; sometimes even applied to the entire diencephalon and called the **optic thalamus**.

As all nervous impulses which reach the brain cortex, except those that come from the olfactory organs, pass through the thalamus, this organ serves as a sort of vestibule for the cortex and probably also as a great relay station for the incoming and outgoing nerves.

It is to be remembered that the optic fibers which occupy the thalamus take up much of that organ, but **it should not be called the optic thalamus** because all fibers to and from the cortex, regardless of whether coming from the eye or not, pass through the thalamus.



B.

Fig. 475.

A, Left lateral aspect of a human brain from which the cerebral hemisphere (with the exception of the corpus striatum, the olfactory bulb and tract, and a small portion of the cortex adjacent to the latter) and the cerebellum (excepting its nucleus dentatus) have been removed. The brain stem (segmental apparatus; palæncephalon) includes everything here shown with the exception of the strip of cortex above the tractus olfactorius and the nucleus dentatus. Within its substance, however, are certain cortical dependencies (absent in the lowest vertebrates), which have been developed to facilitate communication between the brain stem and

Two parts of the thalamus are to be noted. The ventral portion contains chiefly motor coordination centers. In man, this portion is not well developed and is there called the **subthalamus**, which is often confused with the **hypothalamus**.

The dorsal portion of the thalamus is again divided into two portions:

(1) The **primitive sensory reflex centers**, principally in the medial group of thalamic nuclei.

(2) The regular cortical vestibule which forms the **lateral nuclei**. These lateral nuclei are sometimes called the new thalamus (**neothalamus**) to distinguish them from all other portions of the thalamus, which other portions are then called the old thalamus (**palaeothalamus**).

In man, the new thalamus makes up by far the greater portion of that organ. This portion includes "the lateral, ventral, and posterior nuclei (for general cutaneous and deep sensibility) receiving the spinal, trigeminal, and medial lemnisci; the lateral geniculate body and pulvinar (visual sensibility) receiving the optic tracts; the medial geniculate body (auditory sensibility) receiving the lateral or acoustic lemniscus."

It will be noted that Professor Herrick, from whom this quotation is taken, considers the two geniculate bodies as a part of the thalamus, whereas our table calls them the metathalamus. The student will see that all these parts are most intimately connected, and classification is bound to be arbitrary no matter what pains may be taken to make such classification as scientific as possible.

All the lateral nuclei are connected with the cerebral cortex by important systems of fibers running both to and from the cerebral cortex. The fibers themselves are called sensory projection fibers, and all of them pass through or near the internal capsule of the corpus striatum.

While these lateral nuclei receive the impulses from the somatic sensory fibers as well as the deeper sensibility impulses (such as touch, temperature, pain, general proprioceptive sensibility, spatial localization, etc., termed as a whole the somesthetic group), this latter group is probably separately represented in the thalamus, although we have not yet the evidence to demonstrate it.

Each of the chief functional regions in the thalamus is connected with a specific region in the cerebral cortex by its own projection fibers, the tracts being known as **radiations**. For example, there are optic radiations, auditory radiations, somesthetic radiations, etc.

The old thalamus, which comprises the more medial thalamic centers found in lower forms, such as fish, has little or no cerebral cortex,

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the cerebral cortex. The chief of these are found in the thalamus, basis pedunculi, and pons. Compare this with the side view of an intact brain, Figure 473. (From Herrick after Cunningham.)

B, Horizontal section of human cerebral hemispheres. 1, 2, A, H, L, F, etc., Fiber systems.

and seems to retain its function in higher vertebrates. In other words, some "awareness" of what is going on is carried by these medial centers, so that the cerebral cortex is not absolutely necessary for the animal to be aware of its own action or reaction. This means that the cerebral cortex is not necessary for **all**, though it undoubtedly is for most conscious purposes.

Professor Herrick says: "The thalamus can act independently of the cortex in the case of painful sensibility and the entire series of pleasurable and painful qualities; for the thalamic centers when isolated from their cortical connections are found to be concerned mainly with affective experience, and destructive lesions which involve the cortex alone do not disturb the painful and affective qualities of sensation."

**Hypothalamus.** That portion lying immediately beneath the thalamus. A small portion of the primitive neural tube to which the hemispheres are attached has remained in a primitive state, not changing or having any ingrowths or outgrowths. This unchanged portion is called the **pars optica hypothalami**, and, as will be noticed by the table, is a part of the end-brain and not of the diencephalon. The hypothalamus is an important correlation center for olfactory and various visual impulses, including probably the sense of taste.

**Tuber cinereum** is the gray eminence forming the ventral portion of the hypothalamus.

**Infundibulum** is a funnel-shaped extension of the third ventricle, passing through the hypothalamus to the end of the hypophysis (the pituitary body or gland which lies in the sella turcica).

**Mammillary bodies** are a pair of eminences at the posterior end of the tuber cinereum. These bodies are olfactory centers.

**Metathalamus.** The posterior part of the thalamus consists of the **geniculate bodies**. The **lateral** or **external** one is a **visual** center in the thalamus and the **medial** or **internal** body in an auditory center.

**Epithalamus.** This is formed by the membranous choroid plexus (which forms the roof of the third ventricle), the habenula, and the stria medullaris (a fiber-tract which connects the olfactory centers of the habenula and the cerebral hemisphere). The habenula itself is a center for the correlation of olfactory sensory impulses with the various somatic sensory centers of the dorsal part of the thalamus. The **pineal body**, in a very few lower vertebrates, is a sense organ, being called a "parietal eye" (Fig. 476). In the higher forms, this

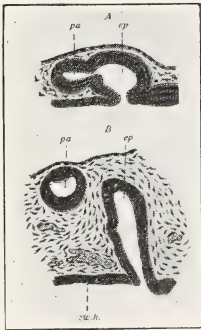


Fig. 476.

Anlage of the epiphysis (pineal gland) and parietal organ in the lizard *Iguana*. A in a 9 day embryo, and B in an 18 day embryo. Longitudinal section. *ep*, epiphysis; *pa*, parietal organ; *zw.h.*, wall of the ventricle in the twist-brain. (After von Klinkowström.)

sensory function has been lost, though it is now supposed to be an organ of internal secretion.

# TELENCEPHALON

In all comparative studies of animals, one must observe lower forms in order that the simpler arrangement there found may furnish an understanding of the more complex adjustment found in the higher forms, as these latter, usually, possess parts that the lower forms possess, plus something additional.

In the study of the nervous system, the dogfish is a good laboratory example with which to work. It has no cerebral cortex developed into immense hemispheres, as in man, which make it so difficult to study the underlying parts and note their relationship (Figs. 477, 478).

In fishes there is a regular system of small sensory canals widely distributed containing sense-organs somewhat similar to those in the semi-circular canals of the internal ear. Their functions are supposed to be somewhat between that of organs of touch in the skin and those of equilibrium of the internal ear. The water vibrations of slow frequency probably make it possible for the animal thus to orient itself. Their innervation comes from the VII, IX, and X pairs of cranial nerves. The

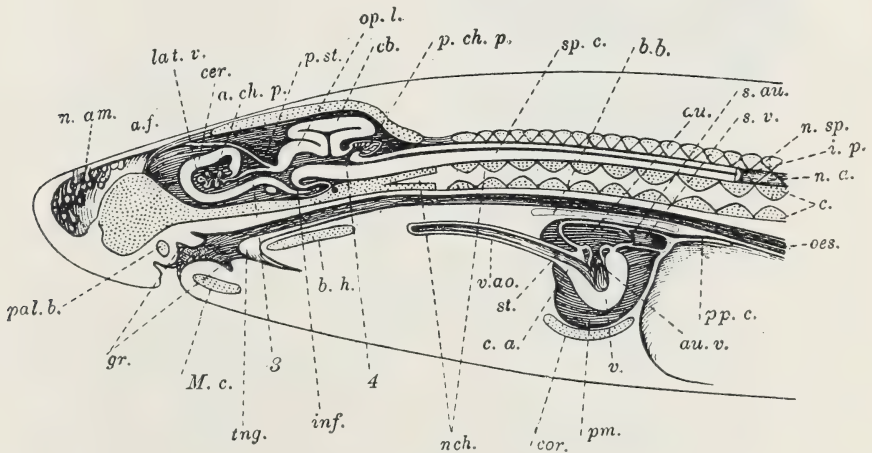


Fig. 477.

A semi-diagrammatic drawing of a longitudinal section through a dogfish, passing slightly to the right of the middle line. *a.ch.p.*, anterior choroid plexus; *a.f.*, anterior fontanelle; *au.*, auricle; *au.v.*, auriculo-ventricular opening and valve; *b.b.*, basibranchial cartilage; *b.h.*, basihyal cartilage; *c.*, centrum; *c.a.*, conus arteriosus; *cb.*, cerebellum; *cer.*, cerebrum; *cor.*, coracoid region of the pectoral girdle; *gr.*, grooves in which the teeth are formed; *i.p.*, intercalary plate; *inf.*, infundibulum; *lat.v.*, lateral ventricle; *M.c.*, Meckel's cartilage; *n.a.*, neural arch; *n.am.*, ampullary sense organs; *n.sp.*, neural spine; *nch.*, notochord; *oes.*, oesophagus; *op.l.*, optic lobe; *p.ch.p.*, posterior choroid plexus; *p.st.*, pineal stalk; *pal.b.*, palatine bar; *pm.*, pericardium; *pp.c.*, pericardio-peritoneal canal; *s.au.*, sinu-auricular opening; *s.v.*, sinus venosus; *sp.c.*, spinal cord; *st.*, semilunar valves; *tng.*, tongue; *v.*, ventricle; *v.ao.*, ventral aorta; 3, third ventricle; 4, fourth ventricle. (From Borradaile.)

sensory canals just mentioned are called **lateral line organs** (Fig. 479) and are absent in higher vertebrates.

If Figure 480 be studied carefully, it will be seen that there is a quite definite area or center for each group of impressions.

The **acoustico-lateral** area is the terminal center of the lateral line nerves as well as of the acoustic nerves (VIII pair).

The general cutaneous area receives impressions from the remaining general exterior of the body.

The nerves from the viscera (that is, from the gills, stomach, etc.) enter a visceral area.

The eye is connected with the optic lobe.

The nose connects with the olfactory bulb and hemisphere. (Some writers have considered the olfactory hemisphere an actual portion of the brain equivalent to the cerebral hemisphere in man. These olfactory hemispheres are, however, only **portions** of the olfactory apparatus.)

The important point is to note that **definite brain regions** are set aside for sensory impressions, and to notice that they are all on the **dorsal surface** (except a part of the olfactory centers).

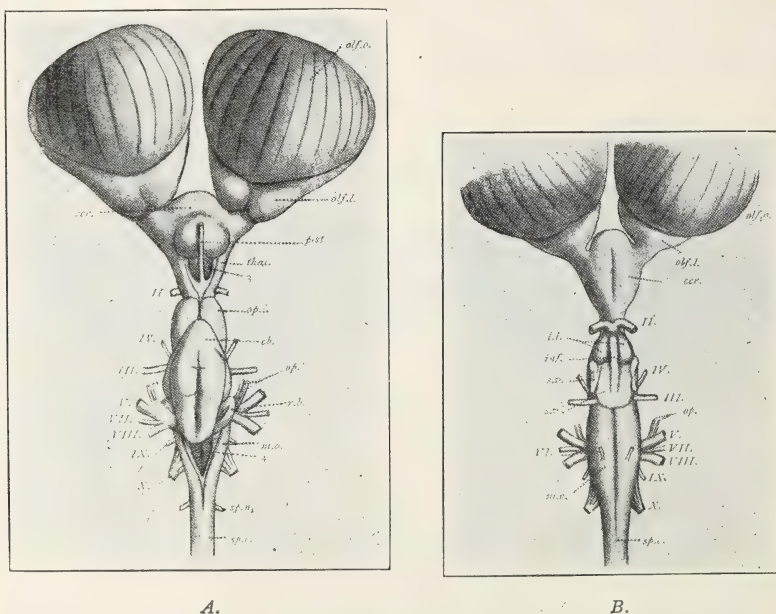


Fig. 478.

A. The brain of the dogfish, seen from above. *cb.*, cerebellum; *cer.*, cerebrum; *m.o.*, medulla oblongata; *olf.l.*, olfactory lobe; *olf.o.*, olfactory organ; *op.*, ophthalmic branches of fifth and seventh nerves; *op.l.*, optic lobes; *p.st.*, pineal stalk; *r.b.*, restiform body; *sp.c.*, spinal cord; *sp.n.*, spinal nerve; *thal.*, thalamencephalon; 3, 4, third and fourth ventricles; *II-V, VII-X*, cranial nerves.

B. The brain of a dogfish, in ventral view. *cer.*, cerebrum; *inf.*, return limb of infundibulum, sometimes regarded as the pituitary body; *li.*, lobi inferiores; *m.o.*, medulla oblongata; *olf.l.*, olfactory lobe; *olf.o.*, olfactory organ; *op.*, ophthalmic branches of fifth and seventh nerves; *sp.c.*, spinal cord; *s.v.*, lateral lobe of saccus vasculosus; *s.v.*, median lobe of the same; *II-X*, cranial nerves. (From Borradaile.)

The regions which Professor Herrick understandably calls "nose brains," "eye brains," "ear brains," "visceral brains," "skin brains," etc., show the simplest type of the pattern of **functional localization of primary reflex centers**. That is, all these special "brains" or **centers** show that practically all of the parts of the brain (except the cerebellum) have a very definite connection with some particular peripheral organs.

This means that this type of simple brain is concerned, in so far as we can tell (with the exception of the cerebellum), only with simple reflex action, there being no large centers for the higher type of adjustment found in the higher vertebrate brains. However, in the higher vertebrates, even including man, there is this same type of simple connection also, but it is obscured by the greatly enlarged correlation centers of which the cerebral cortex is the most important. The distinct course in neurology given in medical schools deals largely and primarily with the histological structure and function of this cortex.

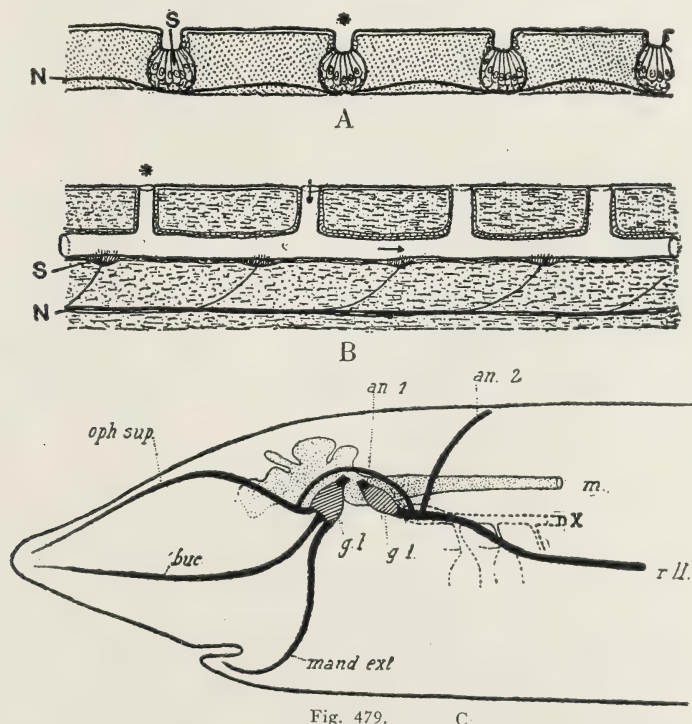


Fig. 479. C

*A* and *B*, Schematic diagrams of sections of the skin. The sections pass through the lateral line organs. *A*, of a Teleost; *B*, of a dogfish. *N*, lateral line nerve; *S*, sensory nerve ending; the asterisk shows the cutaneous orifice; the arrows indicate the direction of the stimulus.

*C*, Lateral line nerve of a fish. *an.1*, anastomosis between the anterior and posterior portions of the lateral nerve; *an.2*, transverse anastomosis between the right and left lateral nerve; *buc.*, buccal branch of lateral nerve; *g.l.*, lateral nerve ganglion; *mand.ex.*, mandibular branch of lateral nerve; *m.*, spinal cord; *oph.sup.*, superficial ophthalmic branch of lateral nerve; *r.ll.*, branch which follows the lateral line *X*, *X* cranial nerve (dotted) to show partial fusion with lateral nerve. (From Vialleton, *A* and *B* after Dean.)

Because the cerebral cortex is found only in the higher forms of vertebrates and, therefore, is supposed to have developed later in the evolutionary scale than the simpler type such as the fish displays, it has been called the **neencephalon** in contradistinction to the fish type of brain which is then known as the old-brain or **palaeencephalon**.

Another point to note is that the "ear brain," the "skin brain," and the "visceral brain" are all contained **in the rhombencephalon**. In fact, the "stem" of the rhombencephalon (also called the segmental portion) is made up of these sensory "brains" and their corresponding motor centers.

This is also true in the higher forms, and the cerebellum (in man, the pons also in a sense) are suprasegmental extensions.

In both lower and higher forms, the "eye brain" includes the **retina** of the eye, the **optic nerve**, and a **part of the roof of the midbrain**. In fish only a few fibers from the optic nerve pass to the thalamus, but in the higher forms, the number of fibers to this portion are many, in fact so many, that the entire thalamus, as stated, is often called the "optic thalamus."

In the fish there are no true cerebral hemispheres, the seemingly similar organs are **hemispheres of the olfactory tract** (with the exception of the very small "somatic area" which becomes the corpus striatum and cerebral cortex in the higher forms). The olfactory apparatus of the fish also embraces the entire epithalamus and hypothalamus.

It follows, from all that has been said, that no nervous impulses can enter the cortex without passing through the reflex centers of the brain-stem first. The brain-stem, therefore, must have all the fibers lying within it which are to carry such impulses. The suprasegmental portions are, therefore, **correlation, coördination, and readjustment centers**.

## DIENCEPHALON

The twixt-brain or inter-brain lies directly in front of the posterior commissure. Still further to the front it is bounded by the **velum transversum** above and the **lamina terminalis** below (Fig. 282, A, C). The cavity in the center is a portion of the third ventricle which extends to the **optic chiasma**. The fiber tracts running from the cerebral hemisphere backward pass into the side walls. Those lying in the dorsal region go through the **thalamus** where there is a large nerve center. The ventral tracts are the cerebral peduncles already mentioned. Directly above and in front of the thalamus is the **epithalamus** which also contains a nerve center known as the **habenula**. The **hypothalamus**, lying as its name implies below the thalamus, consists of the **tuber cinereum** in front and the **mammillary** bodies behind. Both the epithalamus and the hypothalamus bear a relation to the sense of smell and are, therefore,

developed to a greater extent in all lower animals in which this sense is highly developed. Directly behind the velum transversum is the **superior, or habenular, commissure**.

### EPIPHYSIAL STRUCTURES

It is customary to call various parts developed in the roof plate of the primitive fore-brain **epiphysial structures** (Fig. 483, e). Just where the cerebral hemispheres and the twist-brain meet there is a little fold of epithelium, already mentioned, called the **velum transversum**, hanging from the roof of the cerebrum. Directly in front of this is a little choroid plexus called the **paraphysis**. The other epiphysial structures belong to the twist-brain and consist of a **parietal organ** and the **pineal gland** (Fig. 476). Both of these arise from the roof of the twist-brain between the habenular ganglion and the posterior commissure where twist and mid-brains meet. Sometimes they develop as a single outgrowth and sometimes as distinct structures. The more anterior of the two is the parietal organ or eye. The posterior is the pineal gland, also known as the **epiphysis**. These two organs, although varying in the different vertebrates, are usually always present. The parietal organ in at least one group of lizards extends on a slender stalk

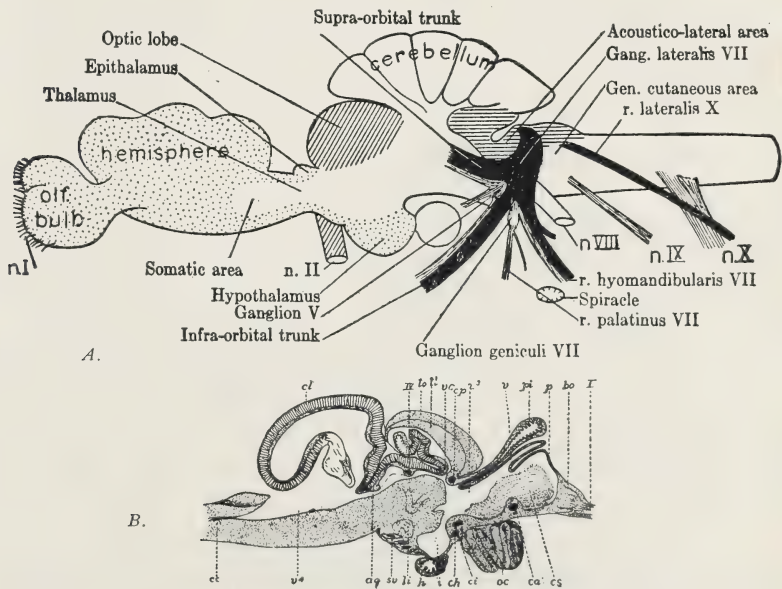


Fig. 480.

A, Side view of the brain of the dogfish *Mustelus canis*. (After Herrick.)  
 B, Longitudinal section of brain of Trout. *ag*, aqueduct; *bo*, bulbus olfactorius; *ca*, *ch*, *ci*, *cp*, anterior, horizontal, inferior, and posterior commissures; *cc*, central canal; *cl*, cerebellum; *cs*, corpus striatum; *h*, hypothysis; *i*, infundibulum; *iv*, trochlearis nerve; *cc*, optic chiasma; *p*, pallium; *pi*, pinealis; *sv*, saccus vasculosus; *tl*, torus longitudinalis; *to*, tectum of optic lobes; *v*, velum transversum; *v*<sup>3</sup>, *v*<sup>4</sup>, ventricles; *vc*, valvula cerebelli. (From Kingsley after Rabl-Rückhard.)

actually passing out of the skull and forming a sort of median eye on the dorsal surface of the head. In those vertebrates in which the parietal organ does not appear at all, the pineal gland seems to show tracts of structure similar to the parietal organ when it does become an eye. It will be remembered that the brow-spot seen on the frog is really the spot where the pineal gland began growing toward the exterior of the body but was cut off by the developing skull.

It is interesting to note that, notwithstanding the close relations of the pineal and parietal organs, the former receives its nerve supply from the posterior commissure, while the parietal organ is connected with the superior commissure of the twixt-brain. All of these structures in the higher vertebrates are completely covered by the cerebral hemispheres growing backward over them. In many of the extinct reptiles there are large **parietal foramina**, and it is supposed that these animals, therefore, had well developed parietal or pineal organs. Directly behind the lamina terminalis there is a chorioid plexus located in the fourth ventricle. This comes from the roof of the brain in this region, and a part of it invades the third ventricle, while another part, the **inferior plexus**, sends branches through the interventricular foramina into the lateral ventricle. This provides a blood supply to the interior portions of the cerebral hemispheres.

A funnel-shaped protrusion from the floor of the diencephalon may be seen posterior and ventral to the optic chiasma, known as the **infundibulum**. This connects with the **pituitary body**, or **hypophysis**, which latter organ has developed from the mouth region. It is encased by the developing skull in a little bony case of its own, called the **sella turcica** (Turkish saddle). The epithelium of the mouth, from which the hypophysis springs, remains connected for a time to that organ, and its point of ingrowth into the brain is called **Rathke's pocket** (Fig. 301, 1). It will be noticed that the pituitary body grows upward from the oral cavity just mentioned, while the infundibulum grows downward from directly behind the optic chiasma to meet it. There are really two parts to the pituitary body, both rich in blood and lymph vessels. The organ is known as a **gland of internal secretion**. Its action is supposed to be connected with the fat-storing powers of the animals; sometimes there is to be found a **postoptic commissure** connecting the ventral parts of the brain in this region.

### MESENCEPHALON

The mesencephalon or mid-brain, as already stated, does not change very much from the way it appears in the embryo. On the dorsal surface there are two lateral swellings, the optic lobes. In mammals these are transversely divided and are called the **corpora quadrigemina**. If they do not divide transversely, they are called **corpora bigemina**. Each optic lobe is connected with fibers from the eye on the opposite side

to which it itself is located. In fishes, the ventricle of the mid-brain is quite large and extends into the optic lobes, but in the higher groups of vertebrates, the ventricle is reduced to a very small opening or **aqueduct**. At the anterior end of the dorsal body of the mid-brain, a band of nerve fibers crosses from one side to the other. Any such cross connections are called **commissures**. These connect the two sides of the central nervous system. Cross fibers of this kind are very numerous in the spinal cord and there are also several in the brain. The one just mentioned is called the **posterior commissure**.

## RHOMBENCEPHALON

### THE CEREBELLUM

The cerebellum, or metencephalon (Figs. 472, 481), is the coördinating organ growing behind the two cerebral hemispheres. The isthmus which connects the mid-brain and hind-brain lies directly in front of the cerebellum. The cephalic anterior wall of the cerebellum meets with the isthmus to form a transverse fold, known as the **anterior medullary velum** (valve of Vieussens), which dips into the fourth ventricle. The median ridge of the cerebellum is known as the **vermis**. This is the only part of the cerebellum which the lower vertebrates possess. In some of the higher reptiles and birds, however, a small outgrowth occurs on each side called the **flocculus**, and it is between the flocculus and the vermis that the cerebellar hemispheres develop in the mammals. This pushes the flocculus ventrad.

Quite a number of fibers grow from one side of the cerebellum to the other on the ventral side of the brain stem. This forms a large transverse band called the **pons** or bridge. The lower vertebrates have only a few fibers of this kind so that the pons is very narrow in them. There is a groove or tract running longitudinally from the cerebellum to the mid-brain along the side of this pons and these lateral tracts are called **anterior peduncles**, while the central or median tract is called the **middle peduncle** or **brachium pontis**. The origin in the cerebellum of the anterior peduncle is called the **nucleus dentatus**.

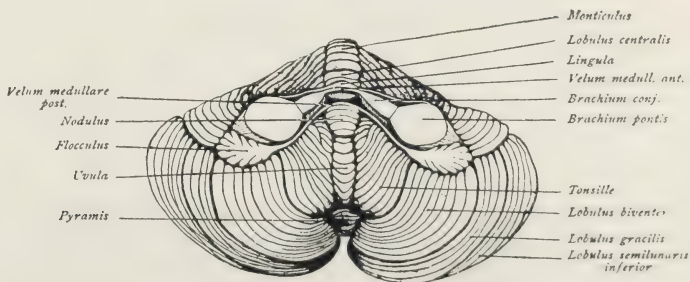


Fig. 481.

Human cerebellum viewed from below and in front. (After Villiger.)

## MEDULLA OBLONGATA

This is a large swelling between the cephalic end of the spinal cord and the brain proper. Various narrow centers appear in the ventral side of the floor serving as centers by which and through which efferent, or outgoing, fibers are redistributed to other nerve cells. The head end of the medulla, by being expanded, forces the various fiber tracts of the dorsal funiculi, as well as of the dorsal part of the lateral funiculi, over to the side of the cerebellum where they enter, bending abruptly inward and forming a cord called the **corpus restiforme**, also known as the **inferior cerebellar peduncle**, on either side. The rest of the fibre tract forms a pair of bands, called **pyramids**, on the ventral surface of the medulla which extend cephalad beneath the mid-brain. These extensions are called the **cerebral peduncles** or **crura cerebri**. They are easily found in the lower vertebrates, but in mammals the pons makes them difficult or impossible to see.

## TELAE CHORIOIDEAE

While the brain is supplied by blood vessels distributed over the outer surface, extensions from the outer vessels push the roof and floors of most of the fore- and hind-brain before them, into the ventricle of these two regions, very much on the same principle as an outgrowth of the digestive tract, such as the liver, pushes its peritoneum-covering before it. These foldings of the plates are called **telae chorioideae**, or **chorioid plexuses**, and it is through these that the nourishing blood passes by osmosis into the ventricle and into the inner surfaces of the brain. It is practically impossible to remove the brain and have the fourth ventricle complete. Usually the chorioid plexus of this fourth ventricle is torn away because it is very thin in this particular region. The large open surface, or cavity, which one sees, when this has been torn away, is called the **fossa rhomboidalis**.

## SUMMARY OF THE BRAIN

### AMPHIOXUS

The brain is extremely small, hardly as large in diameter as the rest of the neural tube. There are but two pairs of cranial nerves, which have been called olfactory and optic, but in so reduced a brain, homologies are uncertain. The sense organs consist of a median olfactory funnel opening into the neurocoele, a median eye-spot (not sensitive to light) on the anterior end of the brain, representing probably a rudiment of paired eyes. The notochord extends the entire length of the body, projecting in front of the brain. This may mean that the brain has retreated from its primitive anterior position. There is no cranium.

## CYCLOSTOMATA

The brain is small but typically vertebrate in structure. The vagus nerve is not included in the cranial region. In the myxinooids, a groove runs the entire length of the dorsal surface. There are four pairs of lobes: (1) olfactory, (2) cerebral hemispheres, (3) mid-brain, and (4) cerebellum. The nasal capsule is enormously developed. The eyes are degenerate and without muscles or nerves. There is only one semi-circular canal in the inner ear. In the lampreys, the cerebral hemispheres are distinct and a band-like cerebellum is recognizable. Eyes are well developed with both muscles and nerves. There are two semi-circular canals in the ear, a condition intermediate between that seen in the myxinooids and that in the true fishes, where three canals are always present.

The flexures are never very well marked and disappear entirely in the adult.

## PISCES

The olfactory organs are paired and end blindly, not communicating with the pharynx as in terrestrial animals and hagfishes. The auditory organs are entirely internal, and have no communication with the exterior. They serve largely as organs of equilibration, though they also receive vibrations. The eyes are much like those of other vertebrates, except that they are lidless and have spherical lenses of short range vision in the water. The brain is small and shows no fissures. Nevertheless, it has all the characteristics of the vertebrate brain, though there are but ten cranial nerves (Fig. 482). The spinal cord is like that in other vertebrates.

## DOGFISH

Although the brain is very small and compact, it is larger in proportion to body size than that of the cyclostomes. The most striking feature is the large size of the olfactory lobes and the slight development of the

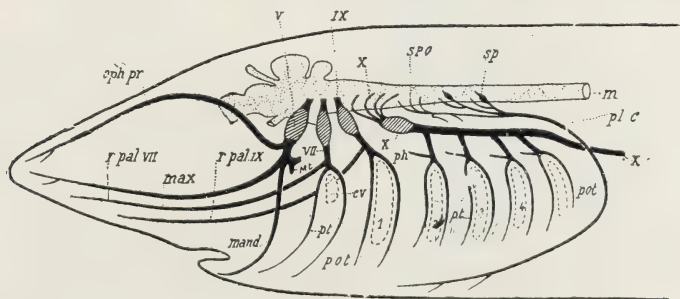


Fig. 482.

Cranial Nerves of the Fish. (Schematic.) *ev.*, spiracle; *mand.*, mandibular branch of the *V*; *max.*, maxillary branch of the *V*; *mt.*, masticator branch of *V*; *m.*, neural cord; *oph.pr.*, deep ophthalmic branch of the *V*; *ph.*, pharyngeal branches of branchial nerves; *pot.*, post-trematic branch; *pt.*, pre-trematic branch; *pl.c.*, cervico-brachial plexus; *r.pal. VII.*, palatine branch of the *VII*; *r.pal. IX.*, palatine branch of the *IX*; *sp.*, spinal nerves; *sp.o.*, spinal-occipital nerves; *V* to *X*, pairs of the corresponding cranial nerves; 1 to 4, branchial slits. (From Vialleton.)

intercerebral fissure. The cerebral hemispheres are well defined, the cerebellum is large, and overlaps anteriorly a part of the optic lobe, and posteriorly a part of the medulla oblongata. The corpora restiformia are large folds on each side of the cerebellum in front and lateral to the rhomboid fossa. The region of the thalamencephalon, from which the optic nerve springs, is comparatively small and slender. The spinal cord is typical and enclosed within cartilaginous neural arches. The dominant sense of the dogfish is olfactory; the sense organs consist of large convoluted invaginations in close contact with the olfactory lobes of the brain. The eyes, although small and probably not especially keen-sighted, are well developed and connected within the brain by a rather slender optic nerve. The auditory organs are enclosed in cartilaginous capsules and consist of three semi-circular canals, a utriculus, and a small simple sacculus. The lateral line sense organs are in grooves of the skin not completely closed. They divide into several branches in the head region, one above and one below the eye, and some in the hyomandibular region.

### TELEOSTS

The vertebral column is not very compact. The vertebrae are often without a centrum or, if a centrum is present, it is an arch-centrum. The nasal tract has no naso-oral groove. It opens by separate nares. The brain has a much reduced cerebrum with all olfactory lobes. The pallium is usually non-nervous, causing the cerebrum to consist largely of the corpus striatum. The cerebellum is larger than a surface view shows, because a great portion projects into the ventricle.

### AMPHIBIA

The cerebrum is larger than the optic lobes, while the olfactory bulb is separated from the cerebrum by a long tract. The various brain parts are quite distinct. In the tailless amphibia, the two halves of the cerebrum are secondarily connected by a transverse band behind the olfactory lobes so that a gap is left farther back.

The telencephalon is larger than in fishes because the pallium is invaded with nervous matter on the inner side. There is no true cortex.

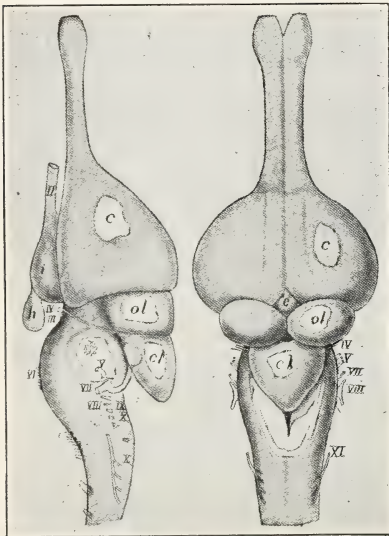


Fig. 483.

Side and dorsal views of young *Alligator*. *c*, cerebrum; *cl*, cerebellum; *e*, epiphysial structures; *h*, hypophysis; *i*, infundibulum; *ol*, optic lobes; *II-XII*, cranial nerves. (From Kingsley after Herrick.)

The optic lobes are large and the pineal gland reaches the cranial roof in the tailless amphibia. In the gymnophiones there is a pontal flexure which brings the pituitary gland beneath the medulla oblongata.

## REPTILIA

There is an advance in the nervous system beyond the amphibia. The cerebral hemispheres are larger and the cerebellum more complete and a cortex is developed. Something of both pontal and nuchal flexures is retained. There may be a beginning of a temporal lobe. A parietal eye is well developed in lacertilia. It is rudimentary in other groups. The olfactory lobes are merged in the hemispheres. The eyes

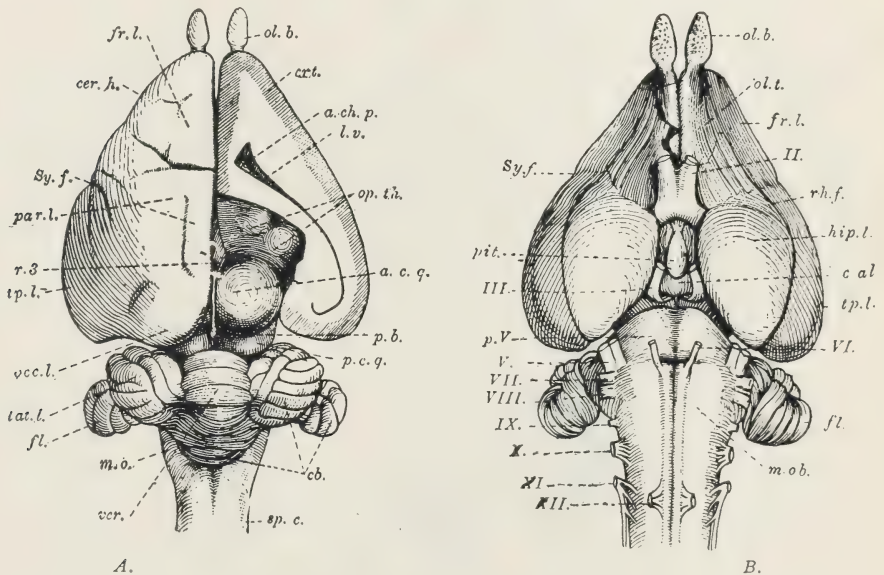


Fig. 484.

A. The brain of a rabbit, seen from above with part of the right cerebral hemisphere cut away. *a.c.q.*, Anterior corpus quadrigeminum; *a.ch.p.*, anterior choroid plexus; *cb*, cerebellum; *cer.h.*, cerebral hemisphere; *crt.*, cortex; *fl.*, flocculus; *fr.l.*, frontal lobe of cerebral hemisphere; *l.v.*, lateral ventricle; *lat.l.*, lateral lobe of cerebellum; *m.ob.*, medulla oblongata; *occ.l.*, occipital lobe of cerebral hemisphere; *ol.b.*, olfactory bulb; *op.th.*, optic thalamus; *p.b.*, pineal body; *p.c.q.*, posterior corpus quadrigeminum; *par.l.*, parietal lobe of cerebral hemisphere; *r.3.*, roof of third ventricle; *sp.c.*, spinal cord; *Sy.f.*, Sylvian fissure; *tp.l.*, temporal lobe of cerebral hemisphere; *ver.*, vermis.

B. The brain of a rabbit from below. *cal.*, corpus albicans; *fl.*, flocculus; *fr.l.*, frontal lobe of the cerebral hemisphere; *hip.l.*, hippocampal lobe; *m.ob.*, medulla oblongata; *ol.b.*, olfactory bulb; *ol.t.*, olfactory tract; *p.V.*, pons Varolii; *pit.*, pituitary body; *rh.f.*, rhinal fissure; *Sy.f.*, Sylvian fissure; *tp.l.*, temporal lobe of the cerebral hemisphere; *III.-XII.*, roots of the cranial nerves. (From Borradaile.)

are small, the pupil round, and the iris unusually dark in color. The thalami develop so far as to reduce the third ventricle to a narrow slit, even causing two edges to unite. This forms the soft commissure, or **intermediate mass**, of the mammalian brain. The sense of hearing is

not very acute. The tympanic membrane is thin and exposed, and is connected with the auditory organ by a slender columellar bone. The sense of smell is the keenest of the senses in the turtle, both in the air and in the water. In correlation with the keen olfactory sense, the olfactory lobes of the brain are highly developed. In the crocodile (Fig. 483), the brain is decidedly advanced in structure for a reptilian brain. The large cerebral hemispheres are especially noteworthy. The tympanic membrane is sunk in a pit. This is a tendency that is carried much further in the birds and mammals.

## AVES

The brain is very short and broad; the cerebrum is large but not convoluted. The cerebellum is very large and complex. All three flexures are partially retained throughout life. The optic lobes are well developed. The olfactory lobes are rudimentary, indicating a poor sense of smell. The olfactory epithelium is poorly developed, and the sense of taste is almost as poorly developed as the olfactory sense. The inner ear, especially the cochlea, is more complex than in reptiles. The eye of birds is large and highly organized, probably keener than that of any other animal. Sclerotic plates cover the eyeball. A fan-shaped pecten (Fig. 490) of unknown function is inserted in the vitreous humor.

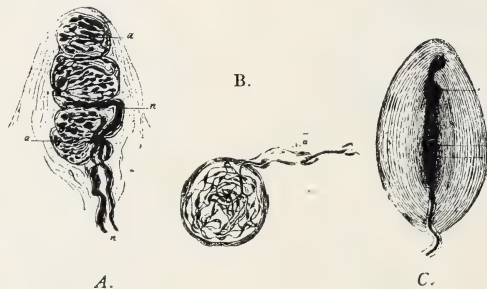


Fig. 485.

Nerve end-organs. *A*, longitudinal section of tactile papilla, containing a Meissner's corpuscle. *B*, Section through a terminal corpuscle (end-bulb of Krause) from the conjunctiva. *C*, Section of a Pacinian corpuscle. The nerve fiber, *n,m*, enters the capsule through the channel *f*, and has its terminal branches at *a*. (*A*, *C*, from Ranvier; *B*, from Dogiel.)

## MAMMALIA

It appears from existing remains that some archaic mammals did not have a more highly developed brain than reptiles. Modern mammals, however, especially the higher groups, have a brain that is much more highly developed than that of all other forms.

In these higher groups the brain is relatively large (Figs. 472, 484),

the cerebral hemispheres showing the greatest increase. The increase is practically confined to the pallium (neopallium).

There is an elaborate system of commissures to connect the two sides of the brain, the corpus callosum being the most important. In fact, the corpus callosum is largest in the highest groups.

In the lower animals, the olfactory lobes lie at the tip of the cerebrum, but in the higher forms the pallial increase pushes the frontal lobes forward so that the olfactory lobes are brought to the lower surface and are separated from the cerebrum proper by a rhinal fissure on each side.

The olfactory tract and the hippocampal tract connect the olfactory lobes with regions farther back, but in man the hippocampal tract is largely rudimentary, the corpus callosum acting as the great connecting region.

The great numbers of fibres from the increased pallium form the **corona radiata** which connects the cortex with the more posterior portions of the brain. And, as connection is made through the thalami, the thalamic regions become greatly enlarged, extend into the third ventricle, and reduce that to a mere slit. Where the two walls come in contact, the intermediate mass is developed.

The mesencephalic lobes are four in number, and are called the corpora quadrigemina, only the anterior pair are connected with the optic nerves, the posterior pair being connected with the sense of hearing.

An important point in the understanding of certain brain structures is the knowledge that the pallium causes a folding so that the original postero-ventral end of the cerebrum, lateral to the pyriform lobe, is pushed below and to the outside of the lateral parts of the hemispheres, the fissure of Sylvius marking the place of folding. It is at the bottom of this fissure that the **island of Reil** is found. This is only the covered part of the sides of the hemispheres.

All higher forms of mammals have the hemispheres arranged in many convolutions. This permits an increase in surface without necessitating a great increase of bulk. However, some animals with less mental ability apparently have more convolutions than the more highly organized, so that it cannot definitely be said that greater convolutions necessarily carry greater mental power.<sup>1</sup>

The mammalian cerebellum, while better developed than that of reptiles, is not so highly developed as that of birds.

**Ornithorhynchus** (Fig. 472) has the most primitive brain of all mammals. It is small, the cerebral hemispheres are smooth and lack all convolutions. This animal is aquatic in its habits, living in stagnant

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<sup>1</sup>*Echidna* has more brain convolutions per body-weight than man.

water and feeding chiefly on mollusks, crustaceans, and worms which it secures by scooping up the muddy bottom with its bird-like bill.

### THE ORGANS OF SPECIAL SENSE

It will be remembered that one of the outstanding characteristics of living matter is its irritability. **Contractility** is usually added to irritability when living protoplasm is discussed. It has already been shown that various functions in the body may be carried on when the entire nerve supply to that portion has been destroyed. We may, therefore, say that, while irritability and contractility are essential parts of living matter, the irritability which causes contractility need not be brought about by a definite system of nerves, although the nerves do carry the stimulus from one part of the body to another to coördinate the various parts and to permit them to work together for some common end.

In all higher forms there are external organs of special sense, such as the nose, the eye, and the ear. In some of the lower forms, such as the earthworm, we found, that while there are no definite eyes, the earthworm nevertheless responds to light thrown upon its body by moving out of the way as rapidly as it can. We know from this experiment that the earthworm is sensitive to light and that, therefore, there are definite sensory regions, more or less specialized, in its skin by which it can receive a stimulus from light.

It would profit an animal little to be able to receive a stimulus if it could not in some way move itself toward or away from such stimulus. The muscles by which an animal may move out of harm's way or toward a food stimulus, and the glands which can secrete substances that will repel an enemy, serve such a purpose.

In order, then, that an animal may profit by the various stimuli it encounters, it must have (1), a **sensory region** or surface of some kind which such stimuli may affect; (2), it must have **an organ**, such as a muscle or a gland, which will permit a reaction to the stimuli, (3), it must have a **conducting mechanism** by which the stimulus may be sent to the reacting organs.

The nerve cells become specialized in structure (or in their manner of connection) in three different ways, namely: (1) they may develop sensitivity and form organs of special sense. These nerve cells then receive specific stimuli. (2) If the nerve cell develops conductivity, it can transmit impulses, such as **sensory**, to the central nervous system, or **motor**, from the central nervous system. The conducting parts formed by this second group of specialized neurons form **nerve tracts**. (3) The third type of specialization of nerve cells is found in the central nervous

system itself. This type forms what are called correlation and association fibres in the sensory field, and coördination fibres in the motor field.

In practically all parts of the skin, there are tiny nerve endings, commonly called **free nerve terminations**, by which the individual recognizes substances when he comes in contact with them.

Then there are certain parts of the tips of the fingers where definite **end organs** are found, and where the sense of touch is quite highly developed. The nerve endings in such special tactile regions are much more complicated than in the simple free nerve terminations. Figure 485 shows some of the various types of these tactile corpuscles.

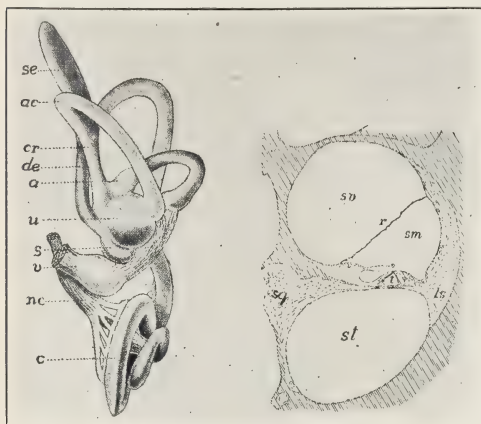


Fig. 486.

*A*, Labyrinth of human embryo, 30 mm. long. *B*, Section through the cochlea of a guinea pig. *a.*, ampullus; *ac.*, anterior canal; *c.*, cochlea; *cr.*, crus; *de.*, endolymph duct; *ls.*, spiral ligament; *nc.*, cochlear nerve; *r.*, Reissner's or vestibular membrane; *s.*, sacculus; *se.*, endolymph sac; *sg.*, spiral ganglion; *sm, st, sv.*, scalae media (ductus cochlearis), tympani and vestibuli; *t.*, tunnel; *u.*, utricle; *v.*, vestibular nerve. (From Kingsley, *A* after Streeter and *B* after Schneider.)

three great divisions of the ear, namely, an external, internal, and middle ear. Of these three portions, the inner ear is the most primitive. All lower vertebrates that develop a definite ear organ at all begin by having simply an **inner ear** (Fig. 19, Vol. I). To this the next succeeding higher forms add the **middle ear** or **tympanum**, while the highest forms add the outer ear.

**The Inner Ear.** This consists of a mere area of thickened ectoderm on each side of the head between the seventh and ninth cranial nerves. A review of the embryology of the ear will recall the cup-shaped auditory vesicle. In the dogfish, the cavity of this remains connected with the exterior by a slender tube known as the **endolymph duct** (Fig. 486). In the frog and in higher forms there is no open auditory cup. There are two layers of ectoderm, the outer one forming an unbroken sheet across the cup. In the dogfish, these endolymph ducts can be seen as external portions on the top of the head.

The distal end of this endolymph duct becomes enlarged, the enlargement being called the **sacculus endolymphaticus**. In the frog and other amphibia, the ducts of both sides often unite dorsal to the brain, while the other parts branch and extend into the spinal canal in a root-like

## THE EAR

In our embryological study we have already discussed the lateral line organs (Figs. 340, 479) which are in all probability tactile, and probably even sound-perceiving organs. In the higher vertebrates there are

manner. In the frog definite diverticula are sent into the so-called calcareous glands surrounding the basal portion of the spinal nerves.

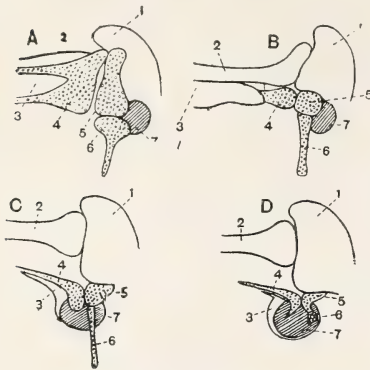


Fig. 487.

Four diagrams to illustrate the variation of ear-bones in Mammalia. The diagrams represent the bones of the back of the lower jaw viewed from the inner side. The tympanic membrane is cross hatched and cartilage bones are covered with small circles, whilst membrane bones are left unshaded.

*A.* Condition in early Theromorphous Reptile. The articular and quadrate are large, and the dentary does not meet the squamosal. *B.* Condition in later Theromorphous Reptile. The dentary has met the squamosal, and the quadrate and articular are reduced in size. *C.* Condition in hypothetical form, the link between Theromorphia and Mammalia. The supra-angular has begun to extend along the border of the tympanic membrane. *D.* Condition in primitive Mammalia (Prototheria). 1. Squamosal. 2. Dentary. 3. Supra-angular. 4. Articular (=Malleus). 5. Quadrate (=Incus). 6. Columella auris (=Stapes). 7. Tympanic membrane. (From Shipley and MacBride.)

The structures of the internal ear, just mentioned, form the **membranous labyrinth** which is filled with a fluid, called endolymph, in which a number of solid particles, called **otoliths**, are found. The otoliths are very tiny crystals of calcium carbonate which cause the endolymph to have a milky appearance. In the true fishes, these tiny crystals have become aggregated into one or more **ear stones** of considerable size. In the dogfish, as the endolymph duct has an opening to the outside, sand from the exterior may also form part of the otoliths.

Cartilage then appears, practically covering the membranous labyrinth. This becomes the **skeletal** (in higher forms the bony) **labyrinth**, and is separated from the membranous labyrinth by a small space filled with a fluid called **perilymph**. As ossification then takes place in the cartilage, the ear bones are formed (Fig. 487). There are two openings into the middle ear, the **fenestra tympani**, also called the **fenestra rotunda**,

The auditory vesicle constricts into two chambers, an upper vestibule or **utricle** and a lower **sacculus**, connected by a narrow **sacculo-utricle canal**. Three outgrowths now take place, one each from the outer, posterior, and lateral walls of the utricle; the one from the lateral wall lies in a horizontal plane, the others in vertical planes. These outgrowths form tubes, and as they are circular in outline, they are called the **semi-circular canals**. Some of the sensory epithelium has spread into all of these regions, but a definite patch of this sensory epithelium can be seen in each of the semi-circular canals, and it is around this patch that the wall of the canal expands to form an **ampulla**. Figure 486 will have to be studied and a model of the ear seen or an ear definitely worked out in one of the animals to make this clear.

In forms higher than fish and amphibia, there is a little pocket, called the **lagna**, given off from the posterior side of the sacculus. Sensory epithelium extends into this pocket, and in the higher forms the lagna becomes a peculiar structure called the **cochlear duct**.

which is closed by a membrane, and the upper opening, known as the **fenestra ovale** or the **vestibule**. The **stapes** (Fig. 487), a small piece of cartilage or bone, is held in place by the membrane.

The lagena grows quite rapidly and coils up into a spiral; in fact, it extends to the skeletal labyrinth, thus dividing the perilymph space into two spiral tubes called **scalae** (Fig. 486). The upper one is called

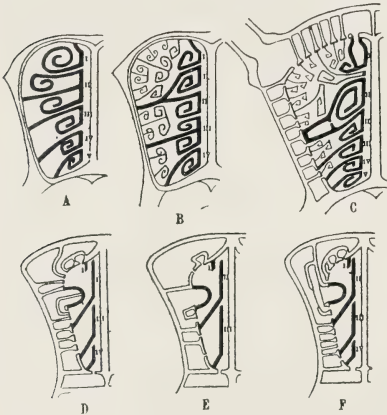


Fig. 488.

Diagrams of ethmoturbinals in Mammals. *A*, Type showing endoturbinalia alone. *B*, Type with endoturbinalia (heavy lines) and two ranks of ectoturbinalia. *C*, Turbinals with pneumatic cavities in the ox. *D, E, F*, three actual cases in man, showing individual variation. (From Wilder after Paulli.)

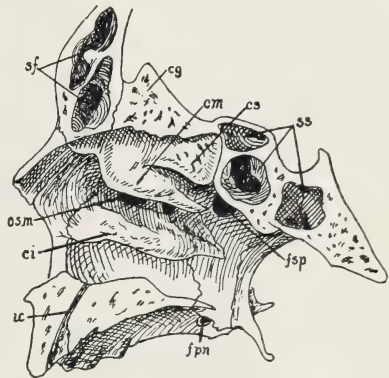


Fig. 489.

Lateral wall of nasal cavity of man. *cg.*, crista galli; *ci.cm.cs.*, inferior, middle and superior conchae; *fpn.*, foramen palatinum majus; *fsp.*, sphenopalatine foramen; *ic.*, incisive canal; *osm.*, opening of maxillary sinus; *sf.*, frontal sinus; *ss.*, sphenoidal sinus. (After Corning.)

the **scala vestibuli**, and the lower the **scala tympani**, while the lagena itself forms the **scala media**, also called the cochlear duct. The bony labyrinth which contains the scala is named the **cochlea**.

As the cochlea only develops in the higher forms, and as our own sense of hearing is very incomplete without this structure, we must come to the conclusion that the lower forms of life, which do not possess such an organ, must either hear entirely different sounds from those we hear, or some other part of the structures they have must do work other than that done in man. A very complicated **organ of Corti** arises within the scala media. Fine hair-like structures develop in the organ of Corti which can only be worked out microscopically and with great difficulty. There is a membrane extending out from the middle wall over some of the hair cells in the organ of Corti, called the **membrana tectoria**. Various functions have been assigned to this membrane, one of them being the ability to recognize pitch in sound. Birds, however, have no organ of Corti at all, and the evidence is quite conclusive that they can distinguish pitch.

The **Middle Ear or Tympanic Cavity**. This first appears in the

**Anura**, that is, in the tailless amphibians, such as the frog. We have already seen from our dissection of the frog that a tympanic cavity connects with the pharynx by a slender duct, the **Eustachian**, or **auditory, tube**. Externally there was a tympanic membrane extending across the fenestra ovale, through which sounds were transmitted to the inner ear. The Eustachian tube is usually considered the homologue of the narrow internal end of the spiracle in the dogfish. Frogs, birds, and reptiles have a chain of ear bones consisting of a columella and stapes; while in the mammals the **incus** and **malleus** replace the columella (Fig. 487).

**The External Ear.** It will be remembered that in the frog the tympanic membrane lies on a level with the surface of the head. In higher forms, the tympanic membrane lies at the bottom of a canal called the **external auditory meatus**. In most mammals, with the exception of those that live in water such as the whales and seals, there is even an **external conch**, developed behind the meatus, to assist in collecting the sound waves and directing them internally. In some birds, feathers are arranged about the external meatus to function as does this conch.

It is to be remembered that the ear not only serves the purpose of taking in and interpreting sounds, but that the semi-circular canals, lying as they do in three dimensions of space and filled with endolymph, function somewhat similar to a carpenter's level, sending sensations to the brain by which the animal recognizes the position of its own body relative to its surrounding environment. We may, therefore, think of the semi-circular canals as an **organ of equilibration**.

## THE NOSE

The real sensory part of the smelling apparatus is always restricted to one or two small patches of olfactory epithelium near the end of the head. As the olfactory sac sinks beneath the surface of the ectoderm, it remains connected by a pair of external openings, called the **nares**. As the dorsal portion of the head then continues growing, the nares are carried toward the tip of the snout or, in the elasmobranchs, toward the ventral side of the head. We have already discussed the forms of nasal capsules in the chapter on the skeletal system. In the higher groups, glands form to keep the epithelium moist.

Beginning with the amphibia and appearing in the higher groups of animals, there is an **accessory olfactory organ**, known as the **organ of Jacobson** (Fig. 339), which is probably used to test the character of food while it is in the mouth. The first and fifth cranial nerves supply the organ of Jacobson, which lies near the internal nostrils.

Cyclostomes have but a single nostril. In all other vertebrates there are paired nostrils, called nares. In the cyclostomes, the nostril is directly connected with the hypophysis, a condition not found in any other vertebrates. In animals living within the water there are folds formed on

one side of each naris, which practically divides it into two; in fact, in many of the teleosts, each primitive nostril is actually divided into two; this permits water to circulate through the olfactory sac, thus carrying various sensations of odors to the extensive sensory surface of the sac.

In air-breathing vertebrates, including lung fishes, unlike water-breathing groups, the nasal cavity has a connection with the alimentary tract. In some elasmobranchs, the first traces are seen of an arrangement for drawing air over the sensory surface. This arrangement is an oro-nasal groove which leads from each nostril to the angle of the mouth (Fig. 296, nas. gr); in fact, this groove may, in some species, form a definite tube. From the lung fishes upward, a similar groove is formed on each side before the skeletal parts form. As this closes, the edges of each groove unite to form a duct leading from the nostril into the oral cavity where an internal naris, or choana, is thus formed. The position of these choanae varies in the different groups of animals. Maxillary and pre-maxillary bones arise ventral to the nasal passage, causing the ducts to appear as though running through the skull.

If the oro-nasal groove does not close, harelip results, just as the failure of the palatines to come together causes a cleft palate.

In some of the urodeles, a projection occurs from the lateral wall. This is one of the first indications of the conchae in the rising groups of vertebrates. Often the ventral portion of the nasal passage is lined only with ordinary epithelium. This portion is then called the **respiratory duct**. The more dorsal portion lining the tract with sensory epithelium is known as the **olfactory duct**. The organ of Jacobson (Fig. 339) is on the medial side of the nasal cavity in the lower urodeles. In the higher urodeles it is ventral, while in the highest it has rotated to the lateral side.

The external nares are closed by the smooth muscles in some of the amphibia. There is little change in the choanae between amphibia and reptiles. The reptiles, however, show a tendency to have a differentiated anterior region known as the **atrium**, or **vestibule**, a middle region connected with the original region, and a posterior region called the **naso-pharyngeal duct**. The naso-pharyngeal duct may vary in length according to whether the choanae are anterior or posterior in position. The crocodiles show an extreme elongation due to the palatines and pterygoids growing inwardly, which causes the internal nares to be pushed to the hinder end of the skull. There is a single concha, which is supported by bone in the lateral wall of the nose of reptiles. This is rather weak, however, in turtles and in the crocodiles. It is divided in front, while a "pseudobranch" develops above and behind the true concha. In snakes and lizards Jacobson's organ is quite an important structure (Fig. 339). It appears as a simple pocket ventral and medial to the nasal cavity near the nasal septum.

In birds there is an anterior and inferior concha vestibuli, and also

a middle and a superior fold, formed by three folds on the wall of each nasal cavity. There is no olfactory epithelium formed on the vestibular conch; it is present on the middle conch immediately before hatching, and disappears immediately after hatching, so that the upper conch is the sole seat of smell in the adult. Jacobson's organ is only found in embryos.

Much greater complication arises in mammals. The naso-pharyngeal duct becomes elongated, while the olfactory area lies directly below a portion of the brain cavity. The interior arrangement of the bones within the nose forms what is called the **nasal labyrinth**. The ethmo-turbinals, the naso-turbinals, and the maxillo-turbinals are the supporting bones, or cartilage, of the folds of the labyrinth. This arrangement permits a great expansion of sensory surface, while the supporting structures keep the folds from touching each other.

In those animals possessing a very slight sense of smell, not only the folds, but the bones themselves, may be reduced.

The maxillo-turbinals and the naso-turbinals arise from the lateral wall of the nasal cavity. The ethmo-turbinals are outgrowths from the ethmoid bone, growing out from the upper hinder part of the septum and extending to the lateral wall. This causes the ethmo-turbinals to insinuate themselves between the hinder ends of the other two. Any of these turbinals may divide in turn. The subdivision of the ethmo-turbinals may be of varying heights so that to form the ecto- and ento-turbinals the naso-turbinals may disappear in the adult. The epithelium of the maxillo-turbinals is not sensory, so that it is assumed that this portion of epithelium serves only to warm and moisten the air in its passage to the lungs. The various forms which the ethmo-turbinals assume in mammals may be seen by a study of Figure 488. Peter gives the following table of homologies of the nasal labyrinth in the amniotes:

- I. Concha of the anterior epithelium: concha vestibuli (birds).
- II. Conchae of the primitive sensory epithelium:
  1. Arising from the lateral wall (conchae laterales).
    - A. Anterior:
      - (a) Primary, ventral: concha of reptiles; middle concha of birds; maxillo-turbinals of mammals.
      - (b) Secondary, dorsal: Upper or posterior of birds; naso-turbinals of mammals (Pseudoconch of crocodiles).
    - B. Arising from the posterior part: conchae obtectae of mammals.
  2. Arising from the primitively median wall: ethmo-turbinals of mammals, numbered from in front backward.

Jacobson's organ (Fig. 339), also called the **vomero-nasal organ**, can be seen in the embryo of most mammals as a pocket on the lower

middle side of each nasal cavity. It opens near the duct from Stenson's gland in rodents and in man, while in other mammals its duct is apparently cut off from the nasal cavity and opens into the naso-palatal canal. Its middle wall is covered with a sensory epithelium to which branches of the olfactory nerve extend. The organ degenerates in adult primates.

There are two kinds of glands in the nasal cavity, known as **Bowman's glands**, which are the smaller, and **Stenson's gland**, which lies in the lateral ventral wall and opens into the vestibule. There are usually sinuses in the bones of the skull connected with the nasal cavity by various openings. Figure 489 shows several of the principal sinuses in the bones, such as the maxillary, frontal, and sphenoidal.

All mammals have an external fleshy nose supported by nasal bones and cartilage, but in swine the fleshy portion forms a proboscis of considerable size, and in the elephant this fleshy proboscis extends tremendously to form the trunk.

It is interesting that while most mammals have a well developed sense of smell, it is not very great in seals, whale-bone whales, and primates, while it is practically absent in the toothed-whales. Often the olfactory nerve disappears entirely.

### THE EYE (Figs. 289, 338)

A review of the embryology of the eye in both frog and chick will make clear how the eye cup, vesicle, stalk, and lens are formed.

A detailed description of the eye must be sought in textbooks of histology. Here we can give but a general outline so as to make intelligible the dissection and comparison of the eye in the various groups of animals studied. The adult eyeball is made up of three tunics, tabulated as follows:

#### I. Tunica Externa.

1. Sclera.
2. Cornea.

#### II. Tunica Media.

1. Choroid coat.
2. Iris.
3. Ciliary body.

#### III. Tunica Interna.

1. Retina.
2. Pigment membrane.

The refracting media or transparent media of the eye, traversed by a ray of light, are:

1. The cornea.
2. Aqueous humor.
3. Lens.
4. Vitreous humor.

Each of these layers is made up of other layers in turn which can be best understood by a careful examination of Figure 18 in Volume I. The retina is made up of several layers of ganglion and sensory cells. The sensory cells lie toward the outside of the eyeball and have a rod or cone toward their outer end. This is the real seeing-portion of the cell. The cells themselves are called rod and cone cells (Fig. 490, C).

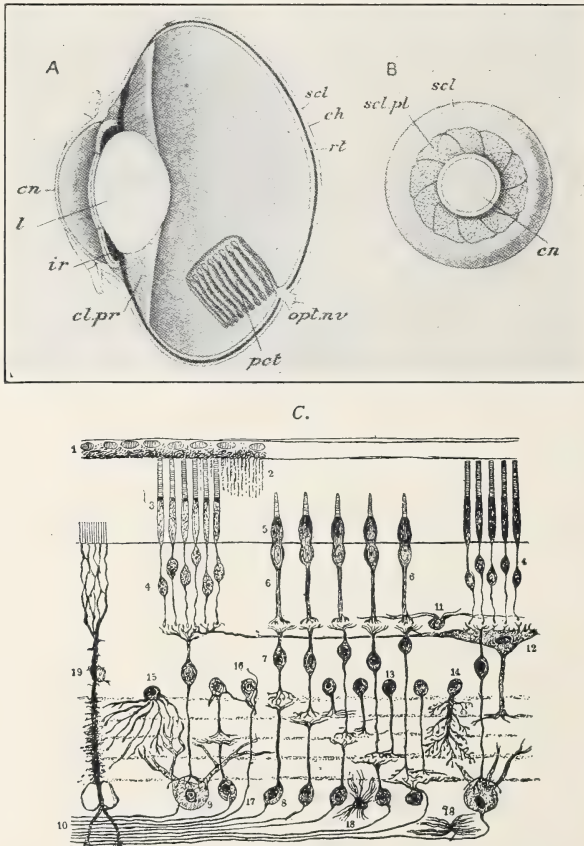


Fig. 490.

*A* and *B*, The eye of *Columba livia*.

*A*, in sagittal section; *B*, entire organ, external aspect. *cn.*, cornea; *ch.*, choroid; *cl.pr.*, ciliary processes; *ir.*, iris; *l.*, lens; *opt.nv.*, optic nerve; *pct.*, pecten; *rt.*, retina; *scl.ps.*, sclerotic plates. (From Parker and Haswell after Vogt and Yung.)

*C*, Schematic representation of the sensory apparatus in the retina of the human eye.

1, Layer of pigment cells next to the choroid; 2, processes of the pigment cells; 3, rods; 4, bodies of rod-cells; 5, cones; 6, axones of cone cells; 7, cone-bipolar cells; 8, 9, ganglion cells; 10, optic nerve fibers (axones of ganglion cells); 11, 12, horizontal cells; 13, 14, 15, 16, cells of different type; functions unknown; 17, fibers (probably axones) of cells having bodies in the brain; 18, neuroglia cells; 19, radial (Müller's) fiber: part of the sustentacular syncytial framework of modified neuroglia.) (From Dunlap after Merkle-Henle.)

The yellow spot at the center of the retina, where vision is most distinct, is called the **macula lutea** or **fovea centralis**.

From what has been said in our general discussion of the central nervous system, we have seen that the surface lining of the central canal of brain and spinal cord is the sensory portion. This is called the **ependyma**. Originally the rods and cones are on the primitive outer surface, and the ganglion cells and nerve fibres are on the ventral surface, of the ectoderm. The rods and cones, therefore, correspond to other sensory organs, such as the organs of the lateral line, taste buds, etc. Now, for the light to get to the rods and cones, it is necessary that such light traverse the whole retina after which the nervous impulses must travel backward through the retinal layer to reach the optic nerve.

It is well at this point to compare the vertebrate eye, which we are now studying, with the parietal eye of the reptiles.

The space between lens and retina is filled with a semi-solid substance called the vitreous humor. What this vitreous substance is and how it arises is still in dispute.

The outer wall of the optic cup forms the pigmented epithelium of the eye; the black pigment developed in this region ultimately surrounds and isolates the rods and cones, so that only light which falls directly upon them can affect them. It is from the outer portion of this pigmented layer that the various tunics of the eye develop. These tunics of the eye are mesenchymal in origin. The tunica vasculosa which surrounds the retina is divided into a **choroid** and a **ciliary portion**. The choroid contains a great many blood vessels and covers the greater portion of the eyeball. It meets the front of the eyeball with the circular ciliary process, in which there are various ciliary muscles by which the lens is moved toward or away from the retina so as to alter its shape. This changes its focal point. The change of focal point is known as the **accommodation of the eye**. The center of the ciliary process is the **iris**, a sort of circular curtain with a central opening. The opening is known as the **pupil**. There are circular muscles, called **sphincter pupillae** and **dilator pupillae**, which contract and enlarge the pupil respectively.

The outer capsule surrounding the various layers just discussed, consists of a **sclera**, which covers the proximal side of the eye, and the **cornea** which is transparent and through which light first passes before reaching the lens. The sclera is usually white and is covered externally in part by the **conjunctiva** which is modified epithelium. In some of the extinct amphibia, and in many of the modern reptiles and birds, portions of the sclera ossify and form a ring of **sclerotic bones**. Snakes and crocodiles, however, do not develop sclerotic bones. In the sturgeon and in many teleosts, there are two or more **dermal bones developed on the sclera**, and in some of the sharks and teleosts there are calcifications to be found also, but these are not true sclerotic bones. Between the lens and the cornea there is an opening, partly divided by the iris into an

**anterior** and a **posterior chamber**. The two chambers are in direct connection through the pupil and are filled with a liquid, called **aqueous humor**.

All that has been discussed so far, in connection with the eye, forms the eyeball proper, the **bulbus oculi**. The eyeball is moved in its socket by six muscles, best understood by studying Figure 466.

Amphibia possess a distinct muscle which draws the eyeball back into its socket. This is known as the **retractor bulbi**. Even some of the jaw muscles may assist in elevating and depressing the ball. In the dogfish there is a cartilaginous rod, called the **optic pedicle**, extending from the eyeball to the skull; this is replaced in the bony fishes by a fibrous band, the **tenaculum**.

The eyelid varies in different groups. The upper and lower, as in the higher vertebrates, and the third lid, called the **nictitating membrane**, usually drawn horizontally across the front from the inner angle of the eye, all form beneath the lower lid. The eyelids themselves have a lining which lies next to the eye and which is a continuation of the conjunctiva already mentioned. In the higher mammals, the nictitating membrane appears as a rudimentary fold, called the **plica semilunaris**, in the inner angle of the eye (Fig. 4, Vol. I).

There are no glands connected with the eye of cyclostomes or fishes. In amphibia, they are of the rudimentary type, but in both reptiles and birds, they are divided into two groups: **Harder's glands** (nictitating glands), lying near the inner angle and the **true lachrymal**, or **tear, glands**, lying in the outer angle.

The tear glands in mammals ultimately come to lie beneath the upper lid and lead, by many ducts, into the conjunctival sac, while Harder's glands degenerate. The tears secreted by the lachrymal glands pass over the conjunctiva and are collected at the inner angle of the eye, where they then pass through the lachrymal duct into the cavity of the nose.

The eyes of the cyclostomes are of a very degenerate type. In the next higher group, namely, the myxinoids, the lens and the eye muscles are lacking, while the iris, and sclera seem quite as one layer.

Fishes have a flattened cornea and a spherical lens and long rods in the retina. There is also a peculiar **falciform process** of vascular and muscular structure that enters the retinal cup through the **choroid fissure** (Fig. 282, B), where it expands. This expansion is called the **campanula Halleri**. As there are no ciliary muscles, it may be that this process serves as a means of accommodation. In the flat fishes, one of the eyes migrates during the embryological development so that both eyes are found on one side of the head (Fig. 371).

In birds and reptiles there is usually a process developed from the inner surface of the retina forming the **pecten** of birds, already described,

while in reptiles it is merely a small cone-shaped process at the point of entrance of the optic nerve. In birds it is quite fan-shaped. Its function is not known, although it is rich in sensory cells.

The pupil varies in mammals, from a vertical slit in cats to a horizontal opening in whales and many ungulates.

The lids may fuse together during embryological development and separate again some time after birth. At the edges of the lids, there are eyelashes or cilia, and immediately interior to these are the ducts of sebaceous glands, called Meibomian or tarsal glands, the glands themselves lying in the substance of the lids.

There is a **retractor muscle** of the eyeball in the ungulates. In most mammals, the **superior oblique muscle** of the eye passes through a loop, known as a **trochlea**, before becoming attached to the eyeball proper.

Eyes may be of various sizes even in mammals. The blind marsupial **Notoryctes** of Australia have neither lens nor differentiation in the cornea, sclera, or choroid, while the retina is lacking in rod and cone cells. In the mole, the eye is quite similar to that of other mammals, but the lids remain fused in the adult.

## THE PERIPHERAL NERVOUS SYSTEM

All nerves running to and from the central nervous system constitute the peripheral nervous system. We have already seen in our embryological study how the spinal nerves have their origin in the neural crests which have been left on each side as the neural tube closed. Figures 470 and 492 show how the dorsal and ventral roots come together before sending out dorsal, ventral, and visceral rami. Not only is the dorsal root of the spinal nerve **sensory** and the ventral root **motor** in action, but each root has two types of nerve fibers within it. These are the **somatic sensory** and the **somatic motor fibers**, which are distributed to the skin as well as to the external sense organs and voluntary muscles. Then there are the **visceral sensory** and **visceral motor fibers** which supply the viscera and circulatory system (Fig. 491). The dorsal and ventral rami, after leaving the connection formed by dorsal and ventral roots, contain mostly somatic fibres with just a few of the visceral type. The visceral ramus contains visceral fibres alone.

In the lower vertebrates, some of the visceral motor fibres actually pass through the dorsal root, so that one cannot in all strictness say that the dorsal root is exclusively sensory. In mammals, dorsal roots are purely sensory, and ventral roots purely motor.

The visceral fibres of the spinal nerves are practically all **efferent**, or **motor**, in function. They do not pass to their terminal organs, such as the smooth muscles, glands, etc., directly, but always end in some sympathetic ganglion where a functional connection is made. From

this ganglion, the impulse is then carried to a peripheral organ by axones from the sympathetic nerve cells.

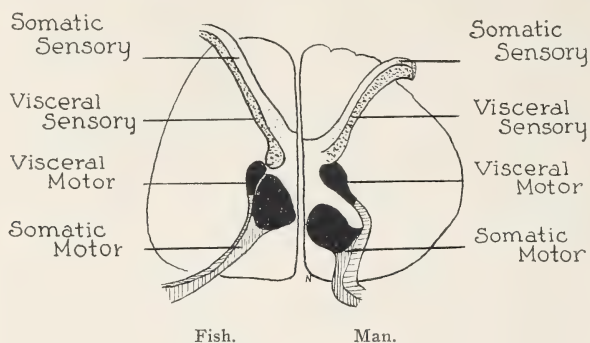


Fig. 491.

Diagram of cross section of spinal cord to show relation of the function of the columns of gray matter to the nerve roots. Left half of the figure is that of a fish and right half that of the spinal cord of man. Note the relatively greater size of the dorsal gray columns and dorsal funiculi in man. This is correlated with the greater importance in man of the ascending connections between the cord and the brain.

In the lower vertebrates, in the regions where the limbs form, usually networks, or **plexuses** are formed. These are paired, as "cervico-branchial" for the fore-limbs, and "lumbo-sacral" for the hind-limbs, while in the higher vertebrates these have separated and there are definite cervical, branchial, lumbar and sacral plexuses. There is usually a great number of nerves (up to about twenty-five) going to form a plexus. In fact, twenty-five is the largest number known, and this occurs in the pectoral fin of skates (Fig. 336).

It is from these plexuses that dorsal and ventral branches of nerves pass out to the two sides of the limbs. In all four-footed animals there is this simple arrangement of a single main nerve trunk on the dorsal and ventral side of the limb, but in mammals there are two nerve trunks on the ventral side of each limb.

As there is also a plexus in snakes and limbless lizards in the regions where limbs usually develop, it is often thought that these animals descended from limbed ancestors, although no trace of limbs occur during their embryological development.

In fishes a connecting nerve, which joins some of the anterior segmental nerves with the limb-stem, passes to the lumbo-sacral plexus. In some fishes, however, not only is there no connecting nerve, but even a plexus is wanting, the spinal nerve entering directly into the limb. The spinal nerves pass to and from the central nervous system, a pair between each two vertebrae. They receive their names from those of the vertebrae immediately anterior to the nerve, with the single exception of the first cervical nerve, which lies between the skull and atlas.

We, therefore, find eight cervical nerves in the neck region, although there are only seven cervical vertebrae. The spinal nerves are then named according to the regions of the spinal column. In man there are twelve **thoracic** spinal nerves, five **lumbar**, five **sacral**, and three to five **coccygeal**.

## THE SYMPATHETIC NERVOUS SYSTEM

There is a great variation in the sympathetic system of various vertebrates. The reason for such variation may be accounted for by the differences of the action and function in the different groups of animals, for it is the sympathetic nervous system which is not under the control of the will, but whose work is the regulation or control, either direct or indirect, of the internal organs, glands, blood vessels, respiratory and reproductive organs. This control is brought about by either stimulating or inhibiting the smooth muscle cells in the walls of the blood vessels, so that by the enlargement or the contraction of the blood vessels a greater or a lesser amount of blood may be supplied to any part. It is also of interest to know that the sympathetic nervous system contains sensory fibres although, when these are stimulated, consciousness of such stimulation does not result.

The sympathetic nervous system is connected with the spinal nerves by the visceral rami. The method of their development has already been discussed in embryology, which should be reviewed at this point (Fig. 337).

In some of the higher groups of animals, large plexuses are formed in the more important and vital body regions. These have received the special names of **cardiac**, **pelvic**, and **hypogastric** ganglia, while the large one in the abdominal region is known as the **solar plexus**.

There is usually a longitudinal sympathetic trunk connecting the chain ganglia of each side, though in the lampreys the chain ganglia are not connected with each other at all, and the sympathetic system is confined entirely to the body cavity, while in slightly higher groups there may be extensions from one to the other ganglion.

Besides the visceral sensory and motor elements which we have been discussing in the sympathetic system, the visceral rami also carry fibres which arise in the ganglion cells of the dorsal ganglion or in the lateral column of the cord itself (Fig. 492). As their axones and dendrites develop, they interlace with both motor and sensory ganglion cells lying in the chain ganglia. Nerve fibres from these then extend out to the viscera, while others run backward in the dorsal and ventral rami of the spinal nerves to reach blood vessels and smooth muscle fibres in the more peripheral regions of the body. These are purely

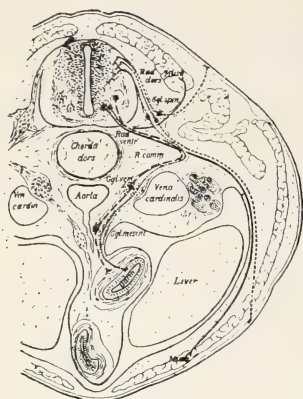


Fig. 492.

Transverse section through the body of a typical Vertebrate, showing the peripheral (segmental) nervous apparatus. *Small dots*, afferent visceral neurones; *coarse dots*, efferent somatic neurones; *dashes*, efferent visceral (ventral root and sympathetic) neurones; *lines*, efferent somatic neurones. *Darm.*, gut; *Ggl. spin.*, spinal ganglion; *Ggl. vert.*, vertebral sympathetic ganglion; *Ggl. mesent.*, mesenteric sympathetic ganglion. The peripheral sympathetic ganglionic plexuses (Auerbach and Meissner) are not shown. *Musc.*, muscle; *Rad. dors.*, dorsal root; *Rad. vent.*, ventral root; *R. comm.*, white ramus communicans. Two sympathetic neurones are represented as intercalated in the visceral efferent pathway. It is doubtful if there should be more than one. (After Frioriep.)

sympathetic fibres, and, as they are non-medullated, they are gray in color, so that the trunk carrying these gray fibres from the chain ganglion to the dorsal and ventral branches is called the gray ramus.

It is important, for future work, to know that some of the cells from the spinal cord or spinal ganglia of the dorsal root migrate to various parts of the body, and are usually quite closely associated with the glands of internal secretion, such as the hypophysis, carotid gland, suprarenals, etc. These cells have a peculiar affinity for chromic acid salts, and are, therefore, often called **chromaffine cells**, though their function is yet unknown.

## THE CRANIAL NERVES

In the early part of our work, we found that the frog has ten cranial nerves, and that mammals have twelve. The cranial nerves differ from the spinal in not being truly segmental nerves (Fig. 493); some of them are purely sensory, some purely motor, and still others are of a mixed nature. Then, too, the cranial nerves which carry sensory fibres, all have a ganglion near the root, while those of a pure motor nature do not.

They are like the spinal nerves in so far as some of them have somatic sensory, somatic motor, visceral sensory, and visceral motor fibres, but are unlike the spinal nerves in that two additional components occur in connection with the cranial nerves. These are the nerves of special sense, and in the fishes, the nerves of the lateral line (Figs. 340, 479).

The somatic sensory nerves in the head are called **general cutaneous nerves**. They terminate in the skin either as free nerve ends or as special sense organs of touch. The visceral sensory fibres end in taste organs, usually inside the mouth, but in some of the teleostomes they are distributed over the surface of the body. The endings, which make up the lateral line arrangements, are sensory, and terminate in little collections of sense cells, commonly called "hillocks" or **neuromasts**, in the ear and in the lateral line organs of certain groups of fishes and amphibians.

The lateral line organs have been thoroughly discussed in the embryology of the frog.

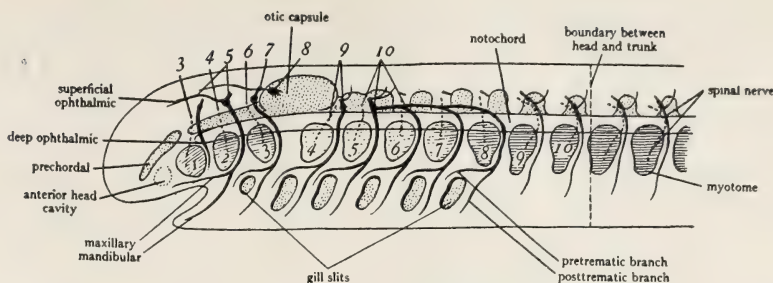


Fig. 493.

Diagram to illustrate the segmentation of the vertebrate head and the relation of the cranial nerves to the segmentation. The numbers above the figure designate the cranial nerves; the numbers in the figure are situated on the head myotomes; the sensory part of the nerves is represented by heavy continuous lines; the motor part by broken lines. The anterior head cavity is the first myotome and therefore the myotome which is numbered 1 is really the second myotome, and so on. But as the myotomes were numbered before the anterior head cavity was discovered, the old numbers are generally retained. The myotomes numbered 1, 2, and 3 produce the eye muscle; those numbered 4, 5, and 6 degenerate in the majority of vertebrates; those from 7 on probably contribute to the tongue musculature but never form typical parietal muscles, such as occur in the trunk. It is seen from the figure that the third cranial nerve and the deep ophthalmic branch of the fifth belong to the first (really second) head segment; the fourth and remainder of the fifth to the second (third) segment; the sixth and seventh to the third (fourth) segment; the ninth to the fourth (fifth) segment; and the tenth to the fifth to eighth (sixth to ninth) segments. The gill slits are intersegmental in location. The relation of the cranial nerves to the gill slits should also be noted. (From Hyman after Goodrich.)

From their functions the cranial nerves may be divided into four groups:

I. Nerves of **special sense**, namely, the **olfactory** and **optic**. These arise in the primitive fore-brain, the olfactory passing to the nose and the optic to the eye.

II. Nerves of the **eye muscles** (Fig. 494), namely, the **oculomotor**, **trochlear**, and **abducens**. These are of the somatic motor type, with a few visceral motor and sensory fibres in the oculomotor. They control the muscles of the eye. It is well to mention the **hypoglossus** at this point, as it belongs to the purely somatic motor group, the spinal accessory being of the visceral motor type.

III. The **acustico-lateralis system**, namely, the **acoustic nerve**, and those portions of the **seventh**, **ninth**, and **tenth** cranial nerves which are connected with the sense organs of the lateral line in the gill-breathing fish and amphibians. These nerves have a separate center in the upper anterior end of the medulla oblongata.

IV. The **fifth**, **seventh**, **ninth**, and **tenth** cranial nerves are more like the spinal nerves than any of the preceding. They all arise in the medulla. Each has a dorsal root and a ganglion, and each contains somatic sensory (general cutaneous) and visceral sensory and visceral motor fibres. The seventh and tenth may also include some of the fibres running to the lateral line. The ninth nerve is the simplest of these, and arises from the dorsal side of the medulla, dividing just behind its

ganglion into two branches, one, the **pre-trematic** (Fig. 482), which passes in front of the gill cleft, and the other, the **post-trematic**, which passes behind that opening. The seventh nerve is arranged in a manner quite similar to that of the ninth, the spiracle being a reduced gill cleft. The fifth nerve, which is also divided in the same way, has its **post-trematic**, called the **maxillary**, and the **pre-trematic** branch, the **mandibular**, the mouth forming the opening about which this nerve

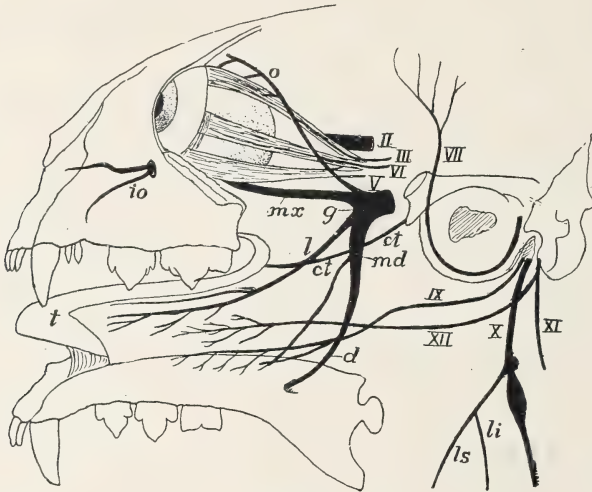


Fig. 494.

Diagram showing cranial nerves of a cat with the lower jaw reflected. II-XII, cranial nerves; *ct.*, chorda tympani; *d.*, dentary nerve; *g.*, Gasserian ganglion; *io*, infraorbital nerve; *l.*, lingual nerve; *li.*, *ls.*, laryngeus inferior and superior; *md.*, mandibularis nerve; *mx.*, maxillaris nerve; *o.*, ophthalmic nerve; *t.*, tongue. (From Kingsley after Mivart.)

divides. The **tenth**, or **vagus**, nerve supplies all of the remaining gill clefts and is, therefore, supposed to be complex, composed of as many nerves as there are clefts behind the first. However, there is no embryological evidence of distinct roots and ganglia.

The cranial nerves are of considerable importance in all physiological, neurological, and pathological work, so it is important that they be thoroughly studied.

I. **The Olfactory Nerve** connects the olfactory lobe of the brain with the sensory epithelium of the nose. It is different from all other cranial nerves in that it consists of many tiny prolongations of the sensory cells themselves, and has no ganglion separate from these cells. The true olfactory nerve consists of these tiny fibres, or threads, extending from the olfactory epithelium in the nose to the so-called mitral cells in the olfactory lobe. The places where the dendrites of the mitral cells meet with the terminations of the olfactory fibres from the olfactory epithelium, are known as **glomeruli**. In the dogfish, for

example, and in many fish, snakes, lizards, and mammals, the true olfactory nerve is very short, but the olfactory lobe is drawn out (Fig. 478), while the distal end of the lobe is enlarged into an olfactory bulb containing the glomeruli, extending proximally from this slender olfactory tract. In these cases, the olfactory bulb lies very close to the olfactory epithelium.

In some fishes, amphibia, lizards, and turtles, the nerve is long, while the olfactory lobe is shortened.

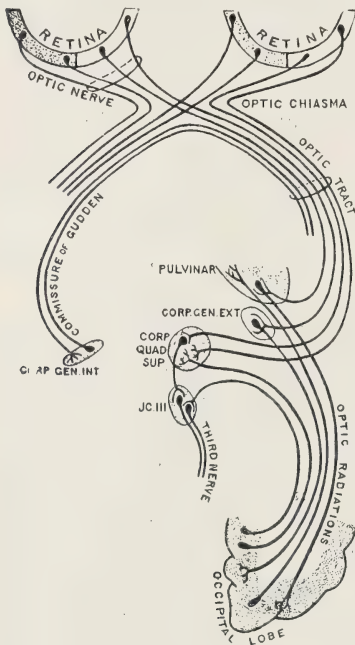


Fig. 495.

Diagram of the central connections of the optic nerve and optic tract to show crossing of the fibers. (From Cunningham's Anatomy.)

It has been found recently that in all vertebrates there is a **terminal nerve**, some times called the pre-optic nerve, which leaves the brain near the base of the olfactory nerve. It has a ganglion upon it, but its functions and connections are as yet unknown.

**II. The Optic Nerve** arises in the eye and extends to the floor of the diencephalon. Branches from it are distributed over the entire inner surface of the retina, the ganglion cells lying in the inner layer. Some of the fibres from the right eye pass to the left side of the brain, and some from the left eye to the right side of the brain (Fig. 495). The crossing of the fibres forms what is called the **optic chiasma**. The fibres, after crossing, extend dorsally and backward into the optic lobe. The optic chiasma is imbedded in the brain of cyclostomes. In other vertebrates it may be plainly seen from the outside. In mammals the crossing in the chiasma is incom-

plete, some of the fibres not crossing. A clear understanding of the growth and development of both olfactory and optic nerves can only be had from an understanding of their embryological development.

There is also a small thalamic nerve which arises between the diencephalon and the mesencephalon. This has so far, however, been seen only in some embryonic fishes. It shortly disappears, and little is known of its function.

The third, fourth, and sixth nerves are the **oculo-motor**, **trochlear**, and **abducens nerves**, or the eye-muscle-nerves, all of which assist in moving the eye in its socket (Fig. 494). The oculo-motor nerve arises from the ventral surface of the midbrain. It supplies the superior, mid-

dle and inferior rectus, and the inferior oblique muscles (Fig. 466). The abducens arises from the inferior surface of the medulla and supplies the lateral rectus muscle. The abducens nerve is often united with the fifth nerve close to its origin. In some very few forms it is absent.

An understanding of how these nerves come to supply the muscles they do in the way that they do, can be had only from our knowledge of the manner in which these muscles originally develop. The eye muscles arise from three myotomes (Fig. 493). One of the somites forms three of the rectus muscles as well as the inferior oblique muscle, while the other two somites form only one muscle each. As the myotome, therefore, divides into four parts, the oculo-motor nerve is carried into each part.

The **trochlear nerve** is the only motor nerve that leaves the dorsal surface of the central nervous system. It has another peculiarity, in that it has a chiasma in the dorsal surface of the midbrain, from which its fibres extend downward to the ganglion cells of the floor of the midbrain.

The nerves of the eye muscles are the only somatic motor nerves in the head of the lower vertebrates.

**V, or Trigeminal Nerve.** The trigeminal nerve is one of the largest of the cranial nerves, and arises from the antero-lateral angle of the myelencephalon. The trigeminal nerve bears a large semilunar or **Gasserian ganglion** (Fig. 494), near its origin. This ganglion may be either just inside or just outside the skull. In all higher vertebrates, the nerve divides into three main branches, known as the **ophthalmic, maxillary, and mandibular branches** (Fig. 494). In the lower vertebrates the maxillary and mandibular nerves may be united for some distance. In the fishes, the **ophthalmic nerve** branches, forming a **superficial** and a **profound ophthalmic nerve**, both of which are purely sensory. In the higher vertebrates, it is the profound ophthalmic nerve which alone persists.

The **superficial ophthalmic** nerve is distributed to the skin, the top of the head, and the tip of the snout. The **profound ophthalmic** nerve passes between the eye muscles to send branches to the eyelids and conjunctiva, and then extends to the mucous membrane of the nose. It is connected with the **ciliary ganglion** to which sympathetic fibres also run. Nerves from this ganglion are sent to the iris and to the ciliary muscles of the eye. The ciliary ganglion controls the smooth muscles of the eye.

The **superficial maxillary** nerve passes along the margin of the upper jaw to supply the face and the teeth. If, however, the profound ophthalmic is reduced, the maxillary nerve extends into the region which the profound ophthalmic usually supplies. In the higher vertebrates, the superior maxillary unites with the sphenopalatine ganglion, to which sympathetic fibres also pass.

The **mandibular nerve** goes to the lower jaw, passing on the outer

side of Meckel's cartilage (Fig. 494). In all higher forms, where the jaws become ossified, the nerve lies within the bone. This nerve carries the motor fibres which innervate the muscles of the jaw as well as the sensory fibres supplying the lips and teeth. In the mammals it also supplies part of the face, and in some of the reptiles a branch, called the **lingual nerve**, is sent into the tongue. In mammals the mandibular nerve is connected with both an **otic** and a **superior maxillary ganglion**, while fibres from the sympathetic system also connect.

It is now thought that the **ophthalmic branches** of the trigeminal nerve really form a distinct nerve, and are not parts of the trigeminus at all. The reason for this belief is that the trigeminal nerve proper arises in the medulla, while certain fibres of the ophthalmic nerve seem to arise in the midbrain.

The trigeminus nerve may also send a twig backward. This is called the **recurrent**, or **lateralis**, of the fifth nerve. This recurrent nerve from the fifth is only found in teleosts and passes to the dorsal side of the jaw near the dorsal fin; in a few fishes it goes into the paired fins.

VII. **The Facial Nerve** arises just in front of the ear, in the medulla. In all higher forms than those which have lateral line organs, there is a single **geniculate ganglion** which is closely associated with the **semilunar** (Gasserian) **ganglion** of the fifth nerve in the fishes and the amphibians. The facial nerve gives off a **palatine** branch running to the roof of the mouth, where it divides into a **pre-trematic** nerve, as already stated, which enters the lower jaw, and a **post-trematic branch**, called the **hyoid nerve**. The hyoid nerve in man is called the **facial nerve**. In all the higher vertebrates a small twig, called the **chorda tympani** (Fig. 494), leaves the hyoid and unites with the mandibular branch of the fifth nerve, after which its fibres enter the lingual branch of the fifth nerve, and go to the taste organs at the tip of the tongue. The remaining portion of the facial nerve is almost entirely motor in function, its fibres controlling the muscles of the neck and the muscles which open the mouth. In mammals that have a large facial musculature the facial nerve is also distributed to other regions of the face.

In animals having organs of the lateral line (Fig. 479), the seventh nerve has an additional ganglion immediately beyond which it divides into three branches, namely, the **superficial ophthalmic**, which usually unites with the superficial ophthalmic of the fifth cranial nerve and then supplies the lateral line organs and related structures on the top of the head dorsal to the eyes. The **buccal nerve**, which supplies the organs below the eye and along the line of the upper jaw, and the **external mandibular** nerve, complete the three branches. The latter is connected to the lateral line organs of the operculum when this is present, and with the lower jaw.

The buccal nerve is usually quite closely associated with the maxil-

lary nerve, while the external mandibular is closely associated with the mandibular ramus of the fifth nerve.

In all higher vertebrates, where no lateral line organs appear, there is no trace of these nerves, even in the embryo, although in the frog and other amphibia which pass through a gilled larval stage, these nerves are outlined in the development, but are lost during metamorphosis.

**VIII. Acusticus (Auditory) Nerve.** This nerve is quite closely related to the facial (Fig. 494), the two ganglia being fused, although the roots are quite distinct. The auditory nerve is entirely sensory, and has two branches, the **cochlear** and the **vestibular**. Both of these are distributed to the sensory structures of the inner ear. Because of the peculiar relations of this nerve to the ear, it is often assumed that, in higher vertebrates, this is the remains of the original lateral line system.

**IX. Glossopharyngeal Nerve.** This is the first of the cranial nerves lying posterior to the ear. It arises from the medulla close to the tenth nerve, and in amphibia, both its roots and its ganglion, called the **petrosal ganglion**, fuse with those of the vagus. In gilled vertebrates the nerve goes to the second gill cleft, there dividing into a **pre-trematic** and a **post-trematic branch**. The pre-trematic passes to the region of the hyoid arch as well as to the oral cavity. In teleosts it also passes to the pseudobranch. The larger of the two branches, the post-trematic, supplies the muscles of the first cleft and sends a single branch to the taste organs, called the **lingual branch**. In amniotes, the post-trematic branch is called the **pharyngeal nerve**, and while there are no gill clefts, the distribution is practically the same as though there were.

There may be a dorsal nerve given off from the glossopharyngeal nerve near the petrosal ganglion, which is somatic sensory in function, and supplies the skin on the upper side of the head. This is quite similar to the **auricular nerve** in mammals. In fishes and amphibia the glossopharyngeal nerve has a connection with the fifth nerve; the connection is called **Jacobson's commissure**.

**X. Vagus or Pneumogastric Nerve.** This is made up of several metameric nerves. In comparative anatomy it is important to remember that in fish and amphibia, this nerve differs considerably from that of the higher forms.

In all gilled vertebrates the vagus arises by a number of tiny roots, while it has two closely associated ganglia, the anterior being called the **lateralis**, and the posterior being called the **jugular**. The jugular ganglion contains both somatic and visceral sensory cells. It is from the jugular ganglion that a **branchio-intestinal** nerve arises, which sends branches to each gill cleft behind the first. In the dogfish there is an **epibranchial ganglion** on each of these branchial nerves. In the higher fishes these ganglia are fused in the main trunk. Beyond the ganglion, each branchial nerve divides into a pre-trematic and a post-trematic

branch, just as does the ninth. Beyond the last cleft, the nerve-trunk continues as the **intestinal nerve**, going to the heart, stomach, and air bladder, when that is present. It is for this reason that the nerve is called **pneumogastric** in human anatomy. The **lateralis part** of the nerve follows the lateral line organs of the body back to the tail sometimes close underneath the skin and sometimes close to the vertebral column.

The lateralis part of the vagus nerve naturally only occurs in gilled animals or those which, like the frog, have gills in their larval stage. In these latter cases the lateral part of the vagus disappears in metamorphosis.

There is a **nodose** (knot-like) **ganglion** lying on the intestinal nerve.

In animals possessing lungs, the musculature of the lungs is also supplied by the vagus. The dorsal ramus of the lower fishes is returned as the **auricular nerve**, and this unites with the auricular branch of the ninth nerve, while **sympathetic connections** are made at various points with the vagus.

It is also important to remember that the nerve supply of an organ is considered the best test of its homology, well shown in the instance of the vagus nerve, which arises in the head region, but is, nevertheless, distributed to the heart, stomach, and lungs. It will be recalled, from our study of embryology that the heart, stomach, and lungs, originally form in the head region of the embryo.

**XI. The Spinal Accessory Nerve.** The eleventh and twelfth cranial nerves **occur only in the amniotes**, although in the dogfish there are twigs from the vagus which innervate the trapezius muscle, while similar conditions are found in amphibia. In the dogfish and the frog, the brain-center for the eleventh nerve is in the medulla oblongata, while in amniotes the center for this nerve lies both in the medulla and in the spinal cord; in fact, some of the more posterior rootlets that go to form the spinal accessory nerve leave the cord as far down as the seventh cervical nerve. These rootlets unite into a trunk that runs cephalad into the cranium between the dorsal and ventral roots of the spinal nerves and then leaves the skull close to the vagus.

The spinal accessory is motor in function, and supplies the trapezius and sternocleidomastoideus muscles which move the shoulder girdle.

**XII. The Hypoglossal Nerve.** This is also a purely motor nerve, although during embryological development, ganglia do appear on the dorsal roots in some mammals, but all these disappear again. The rootlets of the nerve are only two or three in number, although there may be more. These unite to form the hypoglossal nerve. The hypoglossal nerve and the more anterior nerves then unite to form the **cervical plexus**. It is from this plexus that the main trunk goes to the hypo-

glossal muscles as well as to the retractors of the tongue, and, in birds, to the syrinx.

Small **occipital nerves** leave the skull immediately behind the vagus in many fishes. They pass backward and dorsal to the gill clefts and go forward to supply the muscles at the posterior portion of the head, and the muscles of the pectoral fin. It may be that these occipital nerves are homologues of the amniote hypoglossus.

## PRONOUNCING - INDEX - GLOSSARY

### TABLE OF PREFIXES AND SUFFIXES

(To be Memorized)

The object of this Index-Glossary is not to furnish a detailed explanation. This must be sought in the text on the page assigned. The object is to give the student such knowledge of the technical words used in Biology as will enable him to take apart the words he finds in his scientific reading and analyze them. Therefore, he must learn all of the immediately following prefixes and suffixes:

- |   |  |
|---|--|
| <p>A or an (G. prefix, without) e.g. apoda, i.e. without feet.</p> <p>Ab (L. prefix, away from) e.g. aboral i.e. away from the mouth.</p> <p>Ad (L. prefix, toward, upon) e.g. adrenal i.e. upon the renal gland.</p> <p>ae plural-ending for Latin singular nouns ending in A.</p> <p>Ambi (L. prefix, both) e.g. ambidextrous, i.e. ability to use both hands.</p> <p>Amphi (G. prefix, on both sides) e.g. amphibia, i.e. to live on land and in water.</p> <p>Ante (L. prefix, before in place or time) e.g. antebrachium, i.e. placed before the arm.</p> <p>Anti (G. prefix, opposite, or opposed to) e.g. antitoxin, i.e. opposing or neutralizing a toxin.</p> <p>Arch (G. prefix, chief or early) e.g. archenteron, i.e. the earliest enteron or digestive tract.</p> <p>Auto (G. prefix, self) e.g. auto-intoxication, i.e. poisoning produced within one's own body.</p> <p>Bi (L. prefix, double) e.g. bilateral, i.e. same on both sides.</p> <p>Blast (G. either prefix or suffix, a sprout, or bud), e.g. blastoderm, and neuroblast, i.e. a primitive germ-layer and a primitive nerve cell.</p> <p>Brevis (L. short) e.g. adductor brevis, i.e. the short adductor.</p> <p>Caudad (L. tail) used only in an adverbial sense, as growing caudad, i.e. tailward, or toward the tail.</p> | <p>Cephalad (G. head) used only in an adverbial sense, as growing toward the head.</p> <p>Chondro (G. gristle or cartilage) e.g. chondrocranium, i.e. that part of the cranium developing from cartilage.</p> <p>Circum (L. prefix, round-about) e.g. circumoesophageal, i.e. running around the oesophagus.</p> <p>Cleido (L. clavicle—key) e.g. sternocleido mastoid muscle, i.e. the muscle attached to the sternum, clavicle and mastoid bones.</p> <p>De (L. prefix, off) e.g. degenerate, i.e. to become inferior — to lose generative ability.</p> <p>Di (G. prefix, twice) e.g. diploblastic, i.e. to remain in the two-germ-layer state.</p> <p>Dorsad (L. back) used only in an adverbial sense, as toward the back.</p> <p>Ecto (G. prefix, outside) e.g. ectoderm, i.e. the germ-layer lying toward the outside.</p> <p>En (G. prefix, within), e.g. encephalon, i.e. brain—within the cephalon or head.</p> <p>Endo (G. prefix, within), e.g. endoderm, i.e. the germ-layer lying toward the inside.</p> <p>Ento—Same as Endo.</p> <p>Epi (G. prefix, upon) e.g. epinephros, i.e. same as adrenal, namely, lying upon the nephridic organ.</p> <p>Ex (G. prefix, without or outside) e.g. exoskeleton, i.e. having a skeleton on the outside.</p> |
|---|--|

- form (L. suffix, shape) e.g. fusiform, i.e. shaped like a spindle.
- Genetic (G. to produce) e.g. pathogenetic, i.e. to produce disease.
- Hemi (G. prefix, half) e.g. hemisphere, i.e. half a sphere.
- Hyper (G. prefix, above or beyond) e.g. hypertrophy, i.e. an overgrowth.
- Hypo (G. prefix, under) e.g. hypoglossal, i.e. under the tongue.
- Infra (L. prefix, below) e.g. infraorbital, i.e. beneath the orbit.
- Inter (L. prefix, between) e.g. intercellular, i.e. between the cells.
- Intra (L. prefix, within) e.g. intracellular, i.e. within the cell.
- Laterad (L. side), used only in an adverbial sense, as "toward a side."
- lysin (G. suffix, a loosing or dissolving) e.g. bacteriolysin, i.e. a substance which dissolves bacteria.
- Macro (G. prefix, large) e.g. macrocephalon, i.e. a large head.
- Major (L. greater) e.g. pectoralis major, i.e. the greater of the pectoral muscles.
- Mega (G. great) e.g. megaspore, i.e. the larger of the spores.
- Mesiad (G. middle), used only in an adverbial sense, as "to grow mesiad" or toward the center of the body.
- Meso (G. prefix, middle) e.g. mesoderm, i.e. the middle germ-layer.
- Meta (G. prefix, after) e.g. metaphase, i.e. the phase in mitosis coming after the prophase.
- Micro (G. prefix small) e.g. micro-organisms, i.e. organisms not seen by the naked eye.
- Minor (L. lesser) e.g. pectoralis minor muscle, i.e. the lesser pectoral muscle.
- Mono (G. prefix, alone) e.g. monogamy, i.e. marrying but one spouse.
- Multi (L. prefix, many) e.g. multicolored, i.e. many-colored.
- Myxo (G. prefix, slime) e.g. myxophyceae, i.e. slime-algae.
- oid (G. suffix), to be added to make an adjective, e.g. odontoid, i.e. like a tooth.
- Para (G. prefix, beside) e.g. parachordal, i.e. lying beside the notochord.
- Peri (G. prefix, around) e.g. pericardium, i.e. around the heart.
- Poly (G. prefix, many) e.g. polymorphic, i.e. many-formed.
- Post (L. prefix, after) e.g. postbranchial, i.e. behind the gills.
- Pre (L. prefix, before) e.g. pre-oral, i.e. before the mouth.
- Pro (G. prefix, first, or early) e.g. probranchia, i.e. the first gills that form.
- Pseudo (G. prefix, false) e.g. pseudopods, i.e. false feet.
- Retro (L. prefix, backward) e.g. retrolingual, i.e. backward from the tongue.
- Semi (L. prefix, half) e.g. semicircular, i.e. half circle.
- Sub (L. prefix, under) e.g. submandibular, i.e. under the mandible.
- Supra (L. prefix, above) e.g. supratemporal, i.e. above the temporal bone.
- Sur (same as supra) e.g. surangulare, i.e. above the angulare bone.
- Tera (G. prefix, monster) e.g. teratology, i.e. the study of monstrosities.
- Tetra (G. prefix, four) e.g. tetrapoda, i.e. four-footed animals.
- Toxic (G. poison) e.g. toxemia, i.e. toxic + haemia, blood-poison.
- Uni (L. prefix, one) e.g. uniramous, i.e. single branch.
- Ventrad (L. belly) used only as an adverb of direction, as "to grow ventrad."

## INDEX-GLOSSARY\*

In all probability some of the pronunciations, as well as some of the derivations, will not meet with the approval of those who are specialists in Latin and Greek, for, often various forms of words have been used to show the student the varying forms of the same word that he will meet in scientific literature, rather than the same form throughout. Thus, for example, *meros*, thigh, and *meros*, a segment, have both been translated as though they were spelled alike. In Greek, the former has a long "e" and the latter a short "e", which really makes the words totally different.

Then, too, in pronunciation, those who have learned and know a foreign language will always (and rightfully so) pronounce the word as it is pronounced in that language. This makes any definite pronunciation impossible, at least to the exclusion of other pronunciations.

Englishmen learn an Anglicised Latin pronunciation, while Continental Europeans and Americans pronounce their "a" as in lark, "e" as the "a" in lake, and "i" as the "e" in see.

Dictionaries have sometimes used one method and sometimes another. The European is likely to pronounce "c" in such words as *cephalon* as "k", though in America this is not customary, but is sometimes heard.

Not each and every artery, vein, and nerve has been listed separately, as these appear under the more general headings of "Circulatory System" and "Nervous System," but one of a name has been listed so as to show the manner of usage of the definitive word. The same word is often used in different senses. The references cited have been chosen to make these different meanings clear.

If the page number is in italics, the word indexed is to be looked for under the illustration on the page assigned.

Lastly, as this book is written solely for the student, we have used everything which would make matters clearer to him. Therefore, although generally using a consistent marking for the pronunciation, we have also brought in a type of marking which he will find in some of the books, and it is well that he be familiar with it. Such is the case, for instance, in *tiu'ni kay'tah*, for *tū'ni kā'tā*, as it is generally given.

### KEY TO PRONUNCIATION.

ā—as in fate.	ē—as in hen.	ō—as in go.	ow—as in cow.
ä—as in fat.	ê—as in her.	ô—as in not.	û—as in pure.
â—as in far.	ī—as in pine.	ô—as in form.	û—as in nut.
ē—as in he.	î—as in pin.	oi—as in boy.	û—as in French u.

### KEY TO DERIVATIONS.

Ar.—Arabian.	G.—Greek.	L. L.—Late Latin.	O. F.—Old French.
A. S. Anglo-Saxon.	Hind.—Hindustani.	M. D.—Middle Dutch.	O. H. G.—Old High German.
F.—French.	Icel.—Icelandic.	M. E.—Middle English.	P.—Portuguese.
Gael.—Gaelic.	It.—Italian.	M. L.—Middle Latin.	Sp.—Spanish.
Ger.—German.	L.—Latin.	N. L.—New Latin.	Sw.—Swedish.

\* As there is considerable variation in usage when foreign words are pronounced, such pronunciation has been chosen as seemed consistent with the best usage of the language from which the word was taken, as well as from international usage. Consequently, many words are as yet not authoritatively defined as to pronunciation and exact derivation.

It is hoped these may be added in a future edition of this book. The author will, therefore, consider it a favor to receive any and all suggestions which may be of help.

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- EPAXIAL MUSCLES, ěpak'siāl (G. *epi*, upon; L. *axis*, axis), definition of ..... 404
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- EPI-HYAL, ěp'ihī'āl (G. *epi*, upon; *hyooides*, Y-shaped) ..... 314  
Pertaining to the upper portion of the ventral portion of the hyoid arch. As a noun, the upper element of the ventral portion.
- EPIMERE, ěp'imēr (G. *epi*, upon; *meros*, part) ..... 36
- EPIMYOCARDIUM, ěp'imīō'kard'iũm (G. *epi* + *mys*, muscle + *kardia*, heart), definition of ..... 105
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- EPITRICHIMUM, ěp'itrik'iũm (G. *epi*, upon; *thrix*, hair) ..... 242  
An outer layer of the epidermis in the foetus of many mammals, usually shed before birth.
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Sickle-shaped or scythe-shaped.  
Process of eye ..... 454
- FALX CEREBRI, fāks cerebri (L. *falx*, a sickle) ..... 416
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An ensheathing band of connective tissue.
- FASCICULUS, FASCICULI, fa'siku-lus uli (L. a little bundle) .... 405, 414  
The direct pyramidal tract or tracts.
- FASCIOLARIS GYRUS, fas'iolā'rīs jī'rūs (L. *fasciola*, a small bandage) 420
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 Pertaining to the thigh.  
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 The outer and smaller bone of the  
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 Thread-like.  
 FILOPLUME, fil'ōplūm (L. *filum*,  
 thread + *pluma*, feather) ..... 246  
 A delicate, hair-like feather with  
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 Any fringe-like structure.  
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 An embryo in the egg or in the  
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 A capsular fruit which opens on  
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 A gap or space between bones of  
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 Any opening.  
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 An arched sheet of longitudinal  
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 A small cord or band of fibers,  
 especially in the brain.  
**FURCULA**, fur'kiulah (L. a little  
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 A forked process or structure, the  
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 Same as semilunar ganglion.  
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 tā (G. *gnathos*, jaw; *stoma*, mouth)  
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- ICHTHYOSAURS, ik'thiosārs (L. *ichthyosaurus*, fish-like lizards) ..... 275
- IGUANA TUBERCULATA, igwa'na (Sp. *iguana*, from native Haytien name) ..... 231
- ILEUM, definition of ..... 324
- ILIO-COSTALIS MUSCLE, ill'io'kōs'tālis (G. *eilo* + L. *costa*, rib) ..... 406
- ILIUM, ill'eeum—  
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- IMPLANTATION, implanta'shūn (L. *in* + *plantare*, to plant) ..... 200
- INCISOR, insī'sor (L. *incido*, cut into) ..... 279  
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- INCUS, inn'kuss (L. anvil) ..... 446
- INDEX FINGER, in'dex (L. *indicare*, to indicate), definition of ..... 286
- INFRAORBITAL LINE, in'frāōr'bitāl (L. *infra*, below + *orbis*, circle) ..... 158
- INFUNDIBULUM, inn'fundib'yulum (L. funnel).  
(See also hypophysis, pituitary body.)  
Definition of ..... 430  
Of oviduct ..... 16
- INGLUVIES, ingloov'iez (L. *ingluvies*, crop) ..... 321
- INHIBITORY FIBERS, definition of ..... 423
- INNER CELL MASS, in'er (A. S. *inra*, inside), definition of ..... 197
- INNOMINATE, inn'nomm'inate (L. *innominatus*, without a name) .....  
Artery ..... 331
- INSECTIVORA, in'sēktiv'ōrā (L. *insectus* + *vorare*, to devour) ..... 234
- INSULA, in'sula (L. *insula*, island) ..... 418
- INTEGUMENT, integ'ument (L. *intego*, to cover), component parts of ..... 241
- INTERAURICULAR SEPTUM, in'tēr-ōrik'ulār (L. *inter*, between + *auricula*, little ear + *septum*, partition) ..... 116
- INTERBRANCHIAL SEPTUM, in'tēr-brang'kiāl (L. *inter* + G. *branchia*, gills) ..... 334
- INTERCOSTAL ARTERIES, in'tēr-kōs'tal (L. *inter* + *costa*, rib) ..... 367
- INTERMAXILLARY GLANDS (L. *maxilla*, jaw) ..... 318
- INTERMEDIATE CELL MASS (L. *medius*, middle) ..... 169
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- INTERSEGMENTAL ..... 178
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- INTRALIMBRICUS ..... 420
- INTRINSIC MUSCLES, intrin'sik (L. *intrinsecus*, inwards) ..... 406
- INVERSION, OF GERM LAYERS, in-ver'shon (L. *invertere*, to turn about) ..... 199
- INVOLUTION, in'vōlū'shun (L. *involvere*, to roll up) ..... 133
- IRIS, eye'riss (G. rainbow), of eye ..... 451
- ISCHIADIC ARTERY, is'kiād'ik (G. *ischion*, hip) ..... 368
- ISCHIUM, is'kēum (G. *ischion*, hip), Homologue ..... 280
- ISLE, ISLET, OR ISLAND OF REIL ..... 418
- ISTHMUS, OF BRAIN, is'mōs (G. *isthmos*, neck), definition of ..... 421  
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Of pharynx ..... 335  
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- IVORY, of tooth, i'vōri (L. *ebur*, ivory) ..... 308
- JACOBSON'S COMMISSURE, definition of ..... 464
- JACOBSON'S ORGAN, definition of ..... 158, 449  
A diverticulum of the olfactory organ of many vertebrates, often developing into an epithelium-lined sac opening into the mouth.

- JEJUNUM, jee'jew'num (L. hungry), definition of ..... 324
- JUGAL, jew'gal (L. *jugum*, yoke), Malar bone ..... 273
- JUGULAR, jew'giular (L. *jugulum*, the collar bone) ..... 372
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- KIDNEY, kīd'nī (M. E. *kidnere*, kidney), section of ..... 393
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- LABIAL GLANDS, lay'beal (L. *labium*, lip) ..... 318
- LABYRINTH, lāb'irīnth (L. *labyrinthus*, labyrinth) ..... 325
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- Nasal ..... 450
- Of ear ..... 446
- LACERTAE, lās'ēr'tā (L. *lacerta*, lizard), definition of ..... 230
- LACERTILIA, lās'ērt'il'īā (L. *lacerta*, lizard) ..... 229
- LACHRYMAL GLANDS, lāk'rēmal (L. *lacrima*, tear) ..... 158
- LACTEALS, lak'tēalz (L. *lac*, milk) ..... 376
- LACUNAE, lākū'nā (L. *lacuna*, cavity), definition of ..... 43
- LAGENA, lajee'nah (G. *lagenos*, flask), definition of ..... 446
- LAMINA, lamm'eenah (L. a thin plate) ..... 42, 434
- LAMINA TERMINALIS, definition of ..... 146
- LANCELET, definition of ..... 215
- LARVA, lār'vā (L. *larva*, ghost) ..... 123
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- LARYNGEAL CHAMBER, lārīn'jēal (G. *larynx*), definition of ..... 164
- LARYNX, lār'inks (G. *larynx*, gullet), definition of ..... 304
- LATEBRA, lāt'ēbrā (L. *latebra*, hiding-place) ..... 15
- LATERAD. (See table of prefixes and suffixes.)
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- Line organs ..... 432, 433
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- LEMNISCİ, lēmnīs'kī (G. *lemniscos*, fillet) ..... 429
- LENS OF EYE, lēnz (L. *lens*, lentil) ..... 67
- LENTIFORM NUCLEUS, lēn'tifōrm (L. *lens* + *forma*, shape) ..... 427
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- LEPIDOSTEUS OSSEUS, lepp'idoss'teeus (G. *lepis*, scale; *osteon*, bone) ..... 219
- LEVATOR, levay'tor (L. a lifter), definition of ..... 406
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- LIMITING SULCUS, definition of ..... 423
- LINEA ALBA, lin'ēa āl'bā (L. *linea*, line + *alba*, white) ..... 404
- LISSEAMPHIBIA, lis'āmfib'īā (G. *lissos*, smooth; *amphibios*, double life) ..... 223
- LIVER, liv'or (A. S. *lifer*, liver), development of ..... 165
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- LOCALIZATION OF BRAIN CENTERS (L. *locus*, place) ..... 433
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- LONGISSIMUS CAPITIS, lonjiss'eemus cap'itis (L. the longest of the head) ..... 406
- Dorsi ..... 406
- LOPHIUS PISCATORIUS ..... 221
- LOPHODONT, lō'fōdōnt (G. *lophos*, crest + *odont*, tooth) ..... 310
- Having transverse ridges on the grinding surface.
- LUCIDUM, loo'sidūm (L. *lucidum*, clear) ..... 241
- LUNATUM, lūnā'tūm (L. *luna*, moon) ..... 285
- LUNG, lūng (A. S. *lunge*, lung), development of ..... 164
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- LYMPH, limmf' (L. *lympa*, clear water)—
- Duct ..... 356
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- LYMPHOCYTES, lim'fōsīts (L. *lympa* + G. *kytos*, hollow), definition of ..... 376
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- MACULA LUTEA, māk'ulā (L. *macula*, spot + *luteum*, yellow), definition of ..... 453
- MAILED FISHES, definition of ..... 252
- MALACOPTERYGII ..... 219
- MALAR, may'lar (L. *mala*, cheek) ..... 273
- MALLEUS, mahl'eeus (L. hammer) ..... 292, 446
- MALPIGHIAN, māl'pig'ēan (after Malpighi, an Italian biologist). Layer ..... 241
- MAMMA L, mam'mal (L. *mamma*, breast)—
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- MANATUS** .....237
- MANDIBLE**, **MANDIBULAR**, man'dibl, mandib'yular (L. *mandibula*, jaw) .....439
- MANUBRIAL CARTILAGE**, mānū'br'al (L. *manubrium*, handle) .....193
- MANUS**, may'nuss (L. hand), definition of .....284
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- MARSUPIALIA**, marsu'pēā'liā (L. *marsupium*, a pouch), definition of.....233
- MARSUPIUM**, definition of.....195
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- MEATUS**, meā'tus (L. passage), definition of .....448
- MEATUS VENOSUS**, definition of.... 77
- MECKEL'S CARTILAGE**, definition of .....192
- Diverticulum, definition of.....204
- MEDIASTINUM**, mē'diās'tinūm, āstīnūm (L. *mediastinum*, servant).....331
- The space between the right and left pleura in and near the mid-line of the body.
- MEDULLA OBLONGATA**, mēdū'l'a ōb'long'gātā (L. *medulla*, marrow, pith + *oblongatus*, oblong) .....417
- Definition of .....421
- MEDULLARY**, medd'ulayree (L. *medulla*, marrow, pith) .....388
- MEDULLARY CORDS**, definition of.. 96
- MEDULLARY FOLDS**, definition of... 36
- Groove, definition of.....36
- Plate, definition of.....36
- MEDULLATED NERVE FIBERS**, definition of .....414
- MEGALOPS ATLANTICUS**, mēg'ālōps (G. *megalon*, great + *ops*, eye).... 220
- Larval stage of certain crustaceans, conspicuous due to their large stalked eyes. Habitat — Atlantic ocean.
- MEIBOMIAN GLANDS**, mībō'miān, definition of .....249
- MEISSNER'S CORPUSCLE** .....442
- Plexus, a gangliated plexus of nerve fibers in the submucous coat of the small intestine.....458
- MENTAL**, men'tal (L. *mentum*, chin).192
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- MESENCEPHALON**, mēs'ēnsēf'ālōn, (G. *mesos*, middle + *en*, in + *kephale*, head) .....48
- MESENCHYME**, mess'enkime (G. *mesos*, middle + *enchyma*, in a fluid), formation of .....37
- MESENTERIC**, mess'entare'ik (G. *mesos*, middle; *enteron*, gut).....108
- MESENTERIES**, definition of.....113
- MESOCARDIA**, definition of....105, 180
- MESOCARDIUM**, mēs'ōkār'diūm (G. *mesos* + *kardia*, heart), definition of .....46, 352
- MESOCOELE**, mēs'osēl (G. *mesos* + *koilos*, hollow), definition of..... 87
- MESOCOLON**, mēs'oko'lōn (G. *mesos* + *kolon*, large intestine), definition of .....113
- MESODERM**, mess'ohderm (G. *mesos*, middle; *derma*, skin), definition of.. 300
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- MESOGASTER**, mess'ohgas'ter (G. *mesos*, middle; *gaster*, stomach), definition of .....113
- MESOGASTRIUM**, definition of.....322
- MESOHEPATICUM** (G. *mesos* + L. *hepar*, liver), definition of.....180
- MESOMERE**, mess'ohmere (G. *mesos*, middle; *meros*, part), definition of.. 36, 79
- MESONEPHROS** (G. *mesos* + *nephros*, kidney), development of..... 80
- MESORCHIIUM**, messor'keeum (G. *mesos*, middle + *orchis*, testis), definition of .....185, 387
- MESOTIC CARTILAGE** .....190
- MESOVARIA**, definition of.....16, 387
- METACARPUS**, definition of.....284
- METACONE**, mēt'ākōn (G. *meta*, after + *konos*, cone).....312
- The posterior-external cusp of an upper molar.
- METAMERE**, mēt'amere (G. *meta*, after + *meros*, part), definition of.. 36
- METAMORPHOSIS**, mēt'amōr'fōsis (G. *meta*, beyond + *morphe*, form)—
- Of frog .....123
- METAPODIUM**, mēt'apō'diūm (G. *meta* + *pous*, foot), definition of...284

- METATARSUS, mēt'ātār'sūs (G. *meta* + *tarsus*, ankle), definition of. . . . .284
- METATHALAMUS, mēt'āthāl'āmūs (G. *meta* + *thalamos*, chamber), definition of. . . . .430
- METHATHERIA, mētāthē'ria (G. *meta*, beyond + *therion*, a wild beast), definition of. . . . .233
- METRIORHYNCHUS. . . . .259
- MID-BRAIN, definition of. . . . .48
- MID-GUT, definition of. . . . .62
- MILK DENTITION, definition of. . . . .308
- MINIMUS, min'imūs (L. *minimus*, least). The fifth digit, definition of. . . . .286
- MITRAL VALVE, mī'tral (F. *mitre*, a peaked cap), definition of. . . . .362
- MIXED NERVES, definition of. . . . .152
- MIXIPTERYGIUM, mīk'siptērj'ium (G. *mixis*, mixing + *pterygion*, little wing). . . . .283
- MOLAR GLAND, mō'lar (L. *mola*, millstone). . . . .318
- MOLAR TEETH, mō'lār (L. *molere*, to grind). . . . .310
- MOLE. . . . .234
- MONILIFORM, mōnil'ifōrm (L. *monile*, necklace + *forma*, shape). . . . .350
- Constricted at regular intervals, giving the appearance of a chain of beads.
- MONITOR, mō'nitōr (L. *monitor*, one who reminds). . . . .230
- MONKEYS, mung'kis (origin unknown; prob. Fr. G. *mimo*, an ape). . . . .235
- MONODELPHIA, mōnōdēl'fiā (G. *monos*, single + *delphis*, womb). . . . .234
- MONODON MONOCEROS, mōn'ōdon mōnō'serus (G. *monodous*, one-toothed + *monokeros*, a unicorn). . . . .238
- MONOPHYDONT, mōnōfī'ōdont (G. *monos* + *phyein*, to produce + *odous*, tooth), definition of. . . . .309
- MONOTREMATA, mōn'ōtremm'atah (G. *monos*, one; *trema*, opening), definition of. . . . .232
- MONRO—  
Foramen of. . . . .417  
Sulcus of, definition of. . . . .423
- MORGAGNI'S SINUS, definition of. . . . .340
- MORULA, mōr'ulā (L. *morum*, a mulberry), definition of. . . . .25
- Of rabbit. . . . .197
- MOULT, mōlt (L. *mutare*, to change). . . . .243
- MUCOSUM. . . . .241
- MUD-EEL. . . . .225
- MUD-PUPPIES. . . . .225
- Definition of. . . . .225
- MULTANGULUM, mūltāng'gūlum (L. *multus*, many + *angulus*, angle). . . . .285
- Two carpal bones, the trapezium and the trapezoid.
- MUSCLE, mūs'l (L. *musculus*, muscle)—Plate, definition of. . . . .92, 167
- MUSTELIDS, mūs'telids (L. *mustela*, a weasel, also kind of fish), definition of. . . . .311
- MUSTELIS, definition of. . . . .217
- MYELENCEPHALON, mī'ēlēsēf'alōn, (G. *myelos*, marrow + *en*, in + *kephale*, head), definition of. . . . .421
- MYELOCOELE, mī'ēlōsēl (G. *myelos*, marrow + *koilos*, hollow), definition of. . . . .87
- MYLOHYOID, my'lowhigh'oid (G. *myle*, mill; *upsilon*, the letter *y*). . . . .408
- MYOCARDIUM, mī'okār'diūm (G. *mys*, muscle + *kardia*, heart). . . . .45
- Definition of. . . . .105
- MYOCELE, mī'osēl (G. *mys* + *koilos*), definition of. . . . .78
- MYOCOMMATA, mī'okūm'atā (G. *mys*, muscle; *komma*, that which is cut off), definition of. . . . .168
- MYOEPICARDIAL MANTLE, mī'ōēpī-kār'diāl (G. *mys* + *epi*, upon + *kardia*, heart), definition of. . . . .353
- MYOTOME, my'ōtome (G. *mys*, muscle; *tome*, cutting), definition of. . . . .78, 167
- MYSTACOCETI, mis'tācōsē'ti (G. *mystos*, mustache + *ketos*, whale). . . . .239
- An order of cetaceans, including whalebone whales.
- They are toothless but have baleen in upper jaw.
- MYXINE GLUTINOSA, mīksī'nē glūti-nō'sa (G. *myxa*, slime + L. *glutinosus*, gluey). . . . .217
- MYXIPTERYGIUM. . . . .283
- NAIL, nāl (A. S. *naegel*, nail). . . . .245
- The terminal horny plate of finger or toe.
- NARES, nār'ēs (L. *nostril*). . . . .158, 448
- NARWHAL, nār'hwal (Icel. *nāhvalr*, a corpse-whale). . . . .238
- NASAL, nā'zāl (L. *nasus*, nose). . . . .193
- NAVEL, nā'vel (A. S. *nafele*, navel). . . . .208
- Place of attachment of umbilical cord.
- NAVICULARE, navī'k'ūlārē (L. *navis*, ship). . . . .285
- The scaphoid radiale of mammalian carpus.
- NECROBIOTIC GLANDS, nek'rōbiōt'ik (G. *nekros*, a dead body + *bios*, life), definition of. . . . .249
- NECTURUS MACULATUS, nectūr'us (G. *nekτος*, swimming; *oura*, tail). . . . .225
- NEENCEPHALON. . . . .434
- NEOCERATODUS FOSTERI. . . . .222
- NEOPALLIUM, nē'opāl'ium (G. *neos*, young + *pallium*, cloak), definition of. . . . .419, 426

- NEOTHALAMUS, *nēōthāl'āmūs* (G. *neos* + *thalamos*, a chamber), definition of ..... 429
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- NEPHROSTOME, *neff'rowstome* (G. *nephros*, kidney; *stoma*, mouth) .... 81
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- NEURAL, *nū'ral* (G. *neuron*, nerve)—  
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- NEURENTERIC CANAL, *nūr'ēntēr'ik* (G. *neuron*, nerve + *enteron*, gut), definition of ..... 51
- NEUROGLIA, *nū'roglē'ā*, *nūrōg'liā* (G. *neuron* + *glia*, glue) ..... 413  
Supporting tissue of nerve cells and nerve fibers.
- NEUROMASTS, *nū'romāsts* (G. *neuron* + *mastos*, knoll) ..... 458  
Groups of sensory cells in the lateral line of fishes.
- NEUROMERE (G. *neuron* + *meros*, a part) ..... 49, 55  
A spinal segment.
- NEUROPORE, *nūrōpōr* (G. *neuron* + *poros*) ..... 42, 50, 141  
The anterior opening of the neurocoele to the exterior.
- NEWMAN, H. H. .... 119
- NEWTs ..... 224
- NIDAMENTAL GLANDS, *nīd'āmēn'tāl* (L. *nidus*, a nest) ..... 392  
Glands which secrete material for an egg-covering.
- NODOSE GANGLION, *nōdōs* (L. *nodus*), definition of ..... 465
- NOTIDANID, *nōtīd'anīd* (G. *notidanos*, with sharp-pointed dorsal fin) .....  
A sub-order of sharks with more than five gill-clefts.
- NOTOCHORD, *no'tōekord* (G. *notos*, back; *chorde*, string) ..... 138, 216
- NOTOGENESIS, *nō'tōgēn'ēsīs* (G. *notos* + *genesis*) ..... 139
- NOTORYCTES, *nōtōrīktēz* (N. L. same word, a generic name) ..... 455
- NOTOTREMA, *nōtōtrē'ma* (G. *notos* + *trema*, perforation) ..... 392  
A genus of South American toads with dorsal brood-sac.
- NUCHAL, *new'kal* (L. *nucha*, nape of the neck) ..... 278  
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- NUCLEI, OF BRAIN ..... 423
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- NUTRITIVE CELLS, definition of... 387
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- OBSTETRICAL TOAD, *obstet'rikal* (L. *obstetricus*, pertaining to midwifery, from L. *ob*, before, and *stare*, to stand) ..... 226
- OBTURATOR, *ob'tūrātor* (L. *obturare*, to stop up) ..... 279  
Foramen ..... 279
- OCCIPITAL CARTILAGE ..... 191
- OCCIPUT, *ok'siput* (L. *occiput*, the back of the head, from *ob*, over against + *caput*, head) ..... 191
- ODONTOBLASTS, *ōdōnt'ōblasts* (G. *odous*, tooth + *blastos*, a germ) ... 308  
Embryonic cells to form future teeth.
- ODONTOCETI, *ōdōntōsē'ti* (G. *odous*, tooth + *ketos*, a whale) ..... 239  
A sub-order of *Cetacea*.
- ODONTOID, *ōdōnt'oid* (G. *odous* + *eidos*, resemblance, tooth-like) ..... 93  
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- OIKOPLEURA, *oikoplū'ra* (G. *oikos*, house + *pleura*, side) ..... 120  
One of the order *Larvacea*.
- OLECRANON, *ōlēkrā'nōn* (G. *olekranon*, point of the elbow) ..... 287  
Pertaining to a process of the ulna; the elbow.
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- OLFACTORY, *ōlfak'tōrī* (L. *olere*, smell)—  
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- OMASUS, *ōmā'sūs* (L. *omasum*, paunch) ..... 321
- OMENTUM, *ōment'ūm* (L. *omentum*, a fold) ..... 113, 302, 322
- OMNIVOROUS, *omnīv'ōrus* (L. *omnis*, all + *voro*, eat) ..... 312  
Eating both plant and animal food.
- OMOSTERNUM, *ō'mōstēr'num* (G. *omos*, shoulder + *sternon*, breast) .. 277
- OMPHALOMESENTERIC VEIN, *ōm'fālōmēs'ēntēr'ic* (G. *omphalos*, navel + *mesenteron*, mid-gut) ..... 45
- OMPHALOMESENTERIC VS. VITELLINE, *vitēl'īn* (L. *vitellus*, yolk) ... 59

- OOCYTE, ō'ōsit (G. *oon* + *kytos*, cell) 19
- OPAQUE, ōpāk' (L. *opacus*, darkened)  
Impervious to light..... 14
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- OPERCULUM, ōpēr'kūlūm (G. *operculum*, a lid)—  
Of tadpole..... 125, 162
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